FORMAL TITLE to be agreed on

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[Some general phrasing / General problem: Animals require sensory information (about their surrounding) to inform their actions. Acquiring sensory information is challenged in groups, for example by visual blocking or masking of sounds. /// Animals are faced with a overwhelming amount of sensory information and use multiple sensory filtering strategies to focus on behaviourally relevant information only. Such strategies are particulary challenged in social situations, when the actions of group members generate additional temporally and spatially dynamic cues, which might mask or block other information.] Echocating bats emit intense calls and listen for returning echoes to perceive their surroundings/OR: environment. When echolocating in groups, bats may not be able to detect their own echoes due to masking by the intense calls of their neighbours. Bats use a variety of vocalization strategies to cope with 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 developed methods to analyse and extract call parameters of temporally overlapping calls and studied the echolocation of multiple free-flying CF-FM bats of the genus *Rhinolophus* 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 importance of studying behaviour in natural conditions.

## Potential titles

1. Constant-Frequency / High duty cycle bats do not change their echolocation calls in the presence of conspecifics
2. Group-flying CF / HDC bats in the field do not change echolocation call parameters
3. Echolocation remains unaltered in the presence of conspecifics in CF bats
4. Echolocation calls in the field remain unaltered even in groups of CF bats
5. Echolocation calls in the field remain unaltered in the presence of CF bats
6. Conspecifics do not affect echolocation call structure in CF bats

## 1.0 Introduction

Individuals in a group balance the costs and benefits of their membership [@behavecolref]. Groups provide various advantages (increased foraging success, offspring survival, thermoregulation), but also present challenges to individual sensory systems. Lekks, maternal colonies, roosting sites, or even human gatherings are filled with multiple emitted signals – all of which are not equally relevant to a receiver [@principlesofanimalcomm]. Various adaptations to this problem of filtering our irrelevant signals include having unique calls to stand out (eg. mate contact calls in penguins) or synchronizing or avoiding signal overlap (eg. in frog choruses) [@principlesofanimalcomm].

Many studies to date have focused on the sensory challenge of filtering out signals in passive sensing animals (eg. penguins, frogs, crickets), that detect their surroundings by acting as ‘receivers’ of sensory stimuli. The passive nature of a sensory modality has consequences for group members. Visually dominant animals in groups do not majorly affect the ability of other animals to receive light and view their surroundings. In the same vein, a group member receiving a signal does not majorly damp its intensity by the act of listening to it. Individuals in groups of passive sensing animals may thus move (eg. using vision) in the direction of the relevant signal simultaneously while trying to detect it (eg. using audition). For instance, a penguin moving towards its mate in a group is likely using vision, while listening for its mate’s calls. What happens in animals with sensory modalities where mutual interference is unavoidable in groups due to the physics of signal propagation itself?

Active sensing animals like echolocating bats face a unique 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 intense 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 behavioural responses of bats in response to sensory challenge from groups and experimental playbacks. Some bats increase call 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), and/or 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, i.e., the fraction of time spent emitting calls. The first and major group of bats are low-duty cycle bats. They 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, also called CF-FM calls. In contrast to low-duty cycle bats, high-duty cycle bats emit relatively longer calls (10 to 50ms), at much higher duty cycles between 34-57% [@ratcliffereview]. Echolocation duty cycle is directly proportional to the probability of neighbouring 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), a central 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. Species use different frequency bands, and individuals within a species 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). Despite potential temporal overlap of emitted call and returning echo, Doppler-shift compensation spectrally separates the CF parts of the echo and call when a bat is echolocating alone. In groups however, temporal and spectral overlaps between neighbour’s calls and own incoming echoes is bound to occur. Previous investigations [@delREFS]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) developing a methodology to quantify echolocation parameters in the presence of overlapping calls and by 1) studying group echolocation in the understudied high-duty cycle bats and 3) by doing so 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 species emit CF-FM calls with peak frequencies between 102-112 kHz, and are not acoustically distinguishable due to overlap in their call characteristics / frequencies? (Dietz and Kiefer 2016). For the purposes of this study, we thus 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 observed bats that flew in an out of and rested inside a small dome-shaped cave (Figure 1) next to the main entrance of the Orlova Chuka cave system, Bulgaria. The cave had a size of approximately 5 x 3 x 1.6 m3 (l x b x h), one opening where bats flew in and out of throughout the night, and some roosting sites on the inside.

### 2.2 Experimental setup

The placed an experimental audio-video setup inside the cave, consisting of three microphones and two infrared cameras. [I would first describe mics and cams here (as you have mentioned them already), only then followed by the syncing system]

The audio and video feeds were synchronised using the 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).

Two consumer grade CCTV cameras (MODEL etc) with infrared lamps were connected to a digital video recorder (MODEL ect) 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.

Three CM16 microphones (Avisoft Bioacoustics, Glienicke, Germany) were recorded by a 416H soundcard (Avisoft Bioacoustics, 250 kHz sampling rate, 16 bit resolution). As horseshoe bat calls are directional (Matsuta et al. 2013), 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 soundcard was used to record the audio sync signal. Audio was recorded continuously through the night as consecutive multichannel files of 1 minute duration. 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.

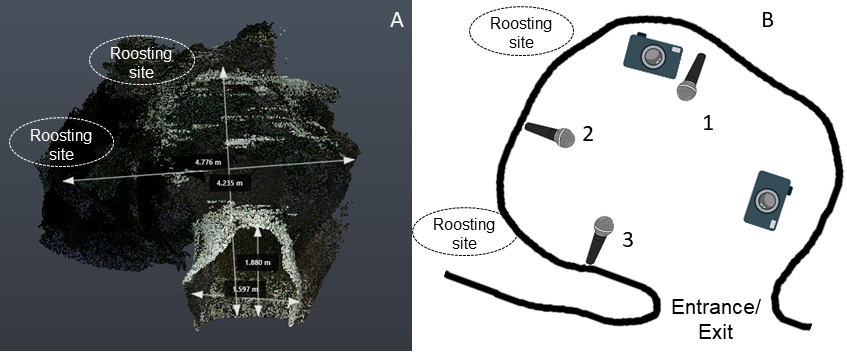


Figure 1: Scan of cave volume and schematic of microphone positions with reference to the entrance/exit and roosting sites of the cave. A) Point cloud scan of the cave as seen with the entrance/exit facing the viewer. (3D scanning by Klaus Hochradel, UMIT Tirol) B) Schematic of the microphone and video 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 MONTH/YEAR. 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.

We recorded 2132 flight bouts of a total duration of xxx, with N single bat flight bouts, and N two – N-bat-flight bouts. …

### 3.2 Matching video annotation to obtain synchronised audio

For each video annotation of a bat flight bout, we matched 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 (55% of all 2132 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 of the three 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 individual echolocation call from each matched audio file. The second analysis is the ‘window’ analysis. Each matched audio was split into consecutive windows of 50 ms duration. We then measured the acoustic parameters per window of all windows of a matched audio file. In recordings with multiple bats, the 50 ms windows could contain 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

Per flight bout, we chose one individual call from the corresponding audio file that was not overlapped by other calls and that had sufficient signal-to-noise ratio (Figure 2) through a random search protocol (SI 3.0). Briefly, from a randomly determined time point, an experimenter began searching into a randomly determined direction (backward or forward in time) until a suitable horseshoebat call was found. Of the 1811 flight bouts, we were able to find 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.

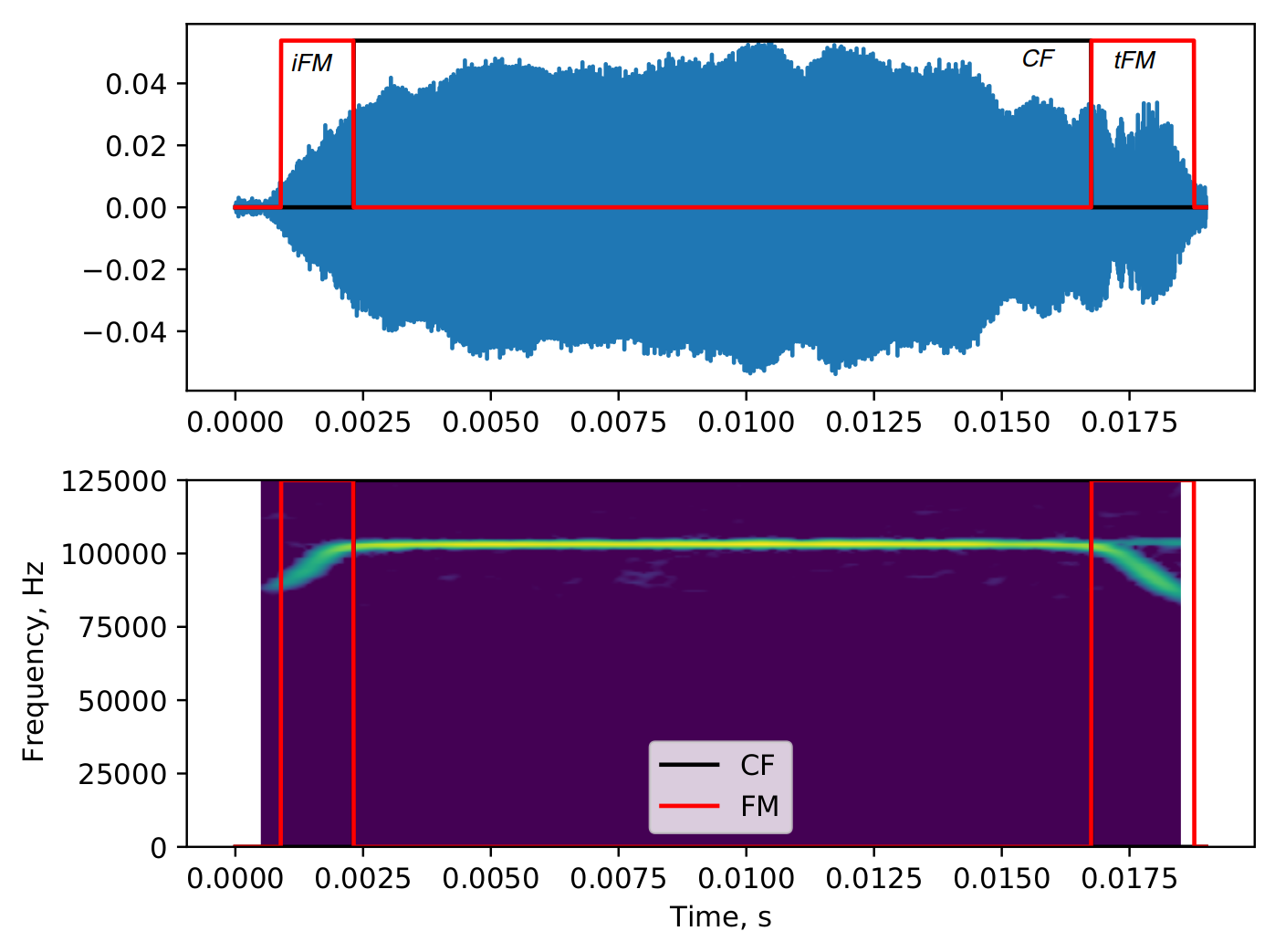


Figure 2: Example of a single manually selected CF-FM call, which was automatically segmented into iFM, CF and tFM regions based on frequency modulation across the call, using the itsFM package. The itsfm package allows accurate segmentation into call parts under challenging recording conditions

From the segmented CF and FM components we measured specific parameters. In the CF component, we measured the peak frequency, RMS level 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 level 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 amplitude ratio between the WHICH PARTS? (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 50 ms windows (SI 4.0). We chose a window duration of 50 ms as it provided high spectral resolution (20 Hz at 250 kHz sampling rate) that allows to distinguish between multiple CF components that may be contained in the window. Initial observations showed that 50 ms was about the longest observed duration of a bat call in our data, and was about twice the length of typical calls.

Over the course of an audio file, there may be multiple windows without calls or very faint calls in them. To exclude those windows, we removed all windows whose RMS level was only up to 20 dB above the (average???) RMS level of manually annotated audio segments without calls (for details, see SI 4.1). From the remaining windows that contained echolocation calls, we calculated the received RMS level, dominant frequencies and FM terminal frequencies. Dominant frequencies are defined as local frequency peaks in the smoothed power spectrum that are within 14 dB of the window’s peak frequency (i.e., the frequency with highest energy in the spectrum). Dominant frequencies are a measurement of the CF frequencies of multiple calls in the same window (for details / detailed methods /for specifics, see SI 4.2). FM terminal frequencies were determined by a spectrogram based method which identified FM regions and chose the lowest frequency in all FM regions identified in a given audio window (SI 4.3). There could be multiple terminal and dominant frequency values for a single window, however only one received RMS level measurement per window. We chose the measurements in the whole audio analysis to be analogous to the measurements in the individual call analyses: the dominant frequencies in the whole audio analysis complements the CF peak frequency measurements in the individual call analysis, while the terminal frequencies and RMS measurements of the FM parts are analogous to the bandwidth and RMS level of the FM parts 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 up to four bats flying in the cave at the same time. However, as the number of recordings of multi-bat group (2 bats) was low (SI 5.0), we combined all annotations with 2 bats into a multi-bat class and compared ‘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 conditions () 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 because the supposed spectral jamming avoidance response, i.e., a shift in the used call frequencies, leads to an increased frequency range (Habersetzer 1981), or, as paradoxically has also been observed, a more narrow range (Furusawa et al. 2012). We performed permutation tests to assess the significance of the observed differences between the group size conditions.

Our dataset consists of calls from a population of resident wild bats of unknown group size. The same bats may have visited the cave site multiple times over the course of a night. Additionally, bat activity was relatively clustered in time, with median time intervals between consecutive flight annotations of 36 s and 54  s, for annotations used in individual call and window analysis, respectively. Thus, our dataset originates from an unknown number of individuals with an unknown amount of pseudo-replication, potentially lowering the variation in the data. To account for this temporal pseudo-replication, we repeated the analysis by creating two independent subsets from our full dataset: The ‘clustered’ subset contained all calls from the annotations that were separated by 1 min from each other. The ‘isolated’ subset contained all calls from annotations that ≥1 min from each other. 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 first calculated the dominant frequency range () across an audio file. We expect variation in the dominant frequency (and thus a non-Zero range of dominant frequency) for multiple reasons: The combined effect of the bat’s Doppler shift compensation and of the Doppler shift due to the bat’s motion relative to the microphone will cause variation in the dominant frequency even for single bats (SI 8.0). In multi-bat and virtual-multi-bat situations, we expect an increase in the range due to multiple bats calling at different individual frequencies. Second, we thus calculated the median difference in dominant frequency range between multi-bat and single-bat and between multi-bat and virtual-multi-bat conditions / trials / observations. 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 measurements of the received level and the terminal frequency potentially correlated received level and terminal frequency measurements from each file. We accounted for this potential file-level pseudo-replication by 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-bat, multi-bat and virtual-multi-bat observations. 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

Signal analysis, data manipulation and visualisation were performed in Python (Van Rossum and Drake Jr 1995) and its 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

### [Here could be a short paragraph describing your general observations of the bat behaviour, as you previously mentioned in the methods]

### 6.1 Individual call analysis

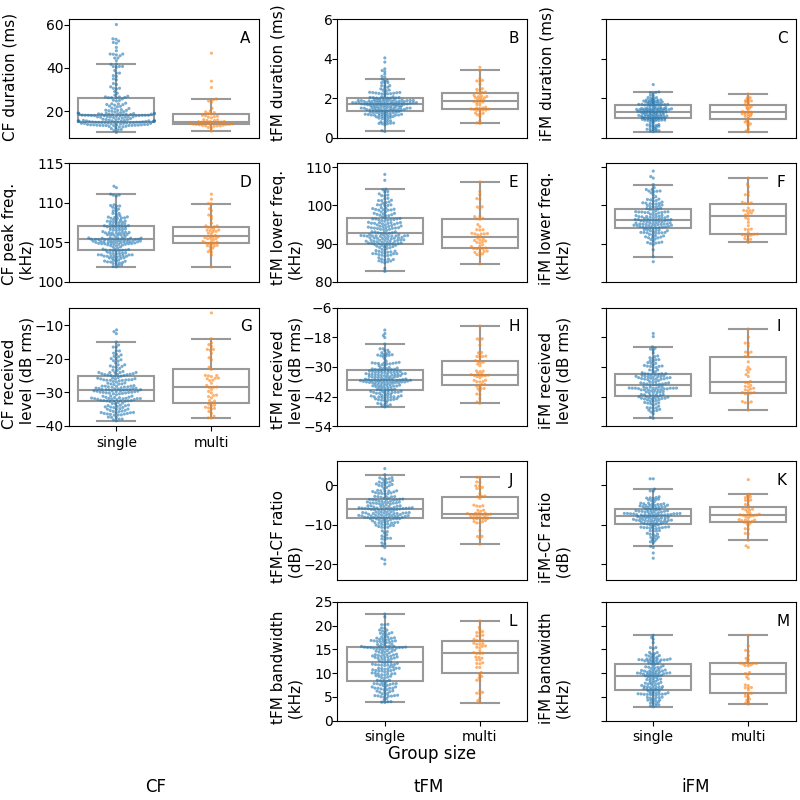


Figure 3: Measured acoustic parameters for the CF, iFM and tFM components of individual calls emitted under single-bat and multi-bat conditions. Each column shows the measurements per call component, while each row shows a group of related measurements: A-C) duration D-F) spectral measurements G-I) received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

We measured 13 acoustic parameters of the initial and terminal frequency-modulated (iFM, tFM) and of the central constant-frequency (CF) component of 226 individual horseshoe bat echolocation calls (Figure 3). Most call parameters showed no difference between single-bat and multi-bat observations (Table 1). Only the median duration of the CF-component was ~3ms shorter (p=0.003) and the median level of the terminal FM-component was ~3 dB fainter (p=0.01) in multi-bat situations compared to single-bat situations. 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,. 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

The dominant frequency range was ~2 kHz larger in multi-bat conditions compared to single-bat condtions (P-VAL, Table 2). 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 |
| Lowest FM frequency (kHz) |  |  | -1.46 | 0.98 |

Dominant frequeny range in (VIRTUAL?)-mutli-bat-situations was slighty increased by ~0.5 kHz compared to XXX-bat situations (Table 3). 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 (<=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.

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