High duty-cycle bats in the field do not alter echolocation calls when flying in groups

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Living in groups has many benefits, but also costs such as the possibility of sensory overload. Large aggregations formed by animals to roost and mate are filled with a multitude of signals of varying relevance to each individual. Here, we focus on groups of echolocating bats, which may experience strong jamming during active sensing . Consequently, several bat species may alter their vocalizations to reduce jamming. We investigate the echolocation behaviour of high duty-cycle constant-frequency bats, which emit long calls with short pauses, while flying in groups in a natural cave environment. Due to their call characteristics, the chances of spectro-temporal overlaps are higher, which increases potential jamming for the bats, and also challenges acoustic measurements. We used synchronised audio-video recordings to count the number of bats and quantify their echolocation in single and multi-bat contexts. To quantify change in echolocation behaviour we develop methods to measure and analyse individual CF-FM calls and groups of overlapping calls. We find no major difference in quantified echolocation parameters between single and multi-bat flights. We thus show that horseshoe bats, despite their long calls that are prone to spectro-temporal overlap, do not alter their calls when flying in groups of up to four bats in a complex echoic cave environment. Our results highlight the robustness of bat echolocation, and the importance of studying behaviour under natural conditions.

**Keywords : active sensing, echolocation, cocktail-party problem, group-living**

For this version COAUTHORS CAN:

#. Reduce word count, we're still \*way\* above 8000 words (~9200 !!!)  
#. Re-work abstract (200 word limit for R Soc Int.   
#. More concrete points:  
 #. In Discussion - not sure what was meant by 'Reference to data possible?'  
 #. try implementing some of the points in the discussion that are pasted raw

OTHER THINGS TO DO:

#. Finalise SI section numbers (They are blank right now on purpose)  
#. Check references for missing entries/typos

# 1 Introduction

Living in groups provides both costs and benefits to the group members (1). From a sensory perspective, group living can be challenging due to the multitude of dynamic sensory information provided by group members, for example in leks, at roosting sites, or at cocktail parties (2,3). As a sender, acoustic signals can be altered to maximise their uniqueness and and intensitywhen in groups. Only a small fraction of all broadcasted information is relevant, and receivers must apply massive filtering and selection during sensory processing and perception to extract relevant information (4,5).. This sensory challenge in groups is becomes particularly serious for animals that perceive their environment by actively radiating energy (9-11), i.e., active sensing animals in the strict sense (7, 8) such as electrolocating fish and echolocating bats.

Echolocating bats emit intense ultrasonic calls and perceive their surroundings by listening for the reflected echoes (12). In groups, however, the faint echoes-of-interest can be buried within the many calls and echoes from neighboring bats (9), due to interference and masking of echoes during auditory processing. To deal with these sensory challenges, bats may increase call levels, alter temporal features such as call rate, duration and duty cycle (13–19), and spectral features such as bandwidth and terminal frequency (20–24). However, there are species-specific and context-dependent differences (14,15,25,26), and increasing evidence challenging the severity of potential jamming (AMICHAI ET AL 2015, CVIKEL ET AL 2015, GÖTZE ET AL 2016, MAZAR & YOVEL 2020, BELEYUR & GOERLITZ 2019). Most of these studies (18,22,29) have been performed in FM-bats, or low duty-cycle bats, which form the majority of all bats (27,30) and emit short and frequency-modulated (FM) calls with long pauses between calls. A second, less speciose group of bats are the CF- or high duty-cycle bats (mostly Rhinolophidae and Hipposideridae), which emit long calls with short pauses. (27). The CF bat call consist of a long constant-frequency (CF) component and one or two flanking short FM-components (CF-FM calls). Since these calls are long (10 to 50ms) with high duty cycles (~30-60 and constant frequency (27), they have a high probability of spectro-temporal overlap of echoes and calls (28).

A typical CF-FM call has up to three call components: a short initial upwards FM sweep (iFM), a long central CF-component (CF), and a short terminal downward FM sweep (tFM) (31). The CF-component is used for prey detection based on a highly resolved frequency analysis in the bat’s auditory fovea (32,33). The CF-frequency differs between species and even individuals (34? ALSO SCHUCHMANN & SIEMERS). CF frequency also varies during flight, where bats lower their emission frequency to compensate for flight-induced Doppler-shifts to keep the returning echo-frequency constant (35,36). When flying alone, this Doppler-shift compensation separates temporally overlapping calls and echoes in frequency space. In groups, however, both temporal and spectral overlap between own echoes, and the calls and echoes of close-by bats is bound to occur. The tFM-component is thought to be involved in target ranging (31,37), while the role of the iFM remains ambiguous. Comparable to call alterations in FM-bats (38), CF-FM bats adjust tFM bandwidth and duration to the behavioural task such as prey capture and landing (31,36,37).

Previous investigations of group echolocation in high duty-cycle CF-FM bats found no support for changes in CF-frequencies to avoid spectral overlap (“jamming avoidance response”)(23,39,40), and only one study quantified changes of the FM-component, reporting increased tFM duration and bandwidth in group flight (23). Even in FM bats the effectiveness of a jamming avoidance response is strongly debated(22, 41). Given the tFM’s flexibility and role in ranging, matching its flexibility (JAMMING REFS) and role (14,20,29) in low duty-cycle bats, there is a strong need for its explicit quantification in multi-bat contexts.

Here, we recorded the activity of two species of horseshoe bats flying in their natural habitat alone and in groups of up to four individuals. Using synchronized audio and video recordings and custom-developed analysis routines, we quantified the effect of group size on multiple temporal and spectral parameters of horseshoe bat echolocation calls. Using two approaches, we analyzed both non-overlapping individual calls as well as multiple overlapping and non-overlapping calls. The analysis of overlapping calls is a nascent field (but see 42), and has, to our knowledge, not yet applied to overlapping CF-FM calls. Based on both analysis approaches, we found major differences in call duration and frequency parameters. Despite their long calls that are prone to spectro-temporal overlap, horseshoe bats seem not to alter their calls when flying in groups of up to four bats in a complex echoic cave environment.

# 2 Methods

## 2.1 Study species and site

We recorded two species of rhinolophid bats, *Rhinolophus mehelyi* and *R. euryale*, in their natural environment over three nights in August 2018. Both species emit CF-FM calls with peak frequencies between 102-112 kHz, and cannot be acoustically distinguished due to CF-frequency overlap (43). For the purposes of this study, we thus treated them as one group of bats, which may face acoustic jamming due to the similarity in spectro-temporal call structure. We observed the bats next to the main entrance of the Orlova Chuka cave system, NE-Bulgaria, where they flew in and out of, and rested inside a small dome-shaped cave (Figure 2.1). The cave had a size of approximately 5 x 3 x 1.6 m (l x b x h), and one opening where bats flew in and out of throughout the night.

## 2.2 Experimental setup

We placed an experimental audio-video setup inside the cave (Figure 2.1), consisting of three microphones and two consumer-grade CCTV infrared cameras (UVAHDBP716, 944x1080 pixels). The cameras were connected to a digital video recorder (XVR1004), which recorded video mostly at 22 Hz(frame rate range 18-27 Hz). Audio from the three microphones (CM16/CMPA, Avisoft Bioacoustics, Germany) was recorded by a soundcard (416H, Avisoft Bioacoustics, 250 kHz sampling rate, 16-bit resolution). The cameras and microphones were placed at different positions, which remained approximately constant across recording nights (Figure 2.1). Video feeds were time-synchronised (but not frame-synchronised) by common time stamps burnt-in on the frame. Audio-video-synchronization was achieved by feeding a random ON-OFF signal into both the soundcard and to a flashing LED recorded on the video (LaurijssenREFNUM; see Supplementary Information (SI) NUM for implementation details). Video was recorded continuously throughout the recording nights , yielding 1.75-8 hours of analysable video, while audio was recorded as consecutive multichannel files of 1 minute duration.



**Figure 1: Experimental cave site and set-up for audio-video recordings:** (A) Point cloud scan and (B) schematic of the cave, indicating the opening, typical roosting sites, and the positions of microphones and cameras (3D scanning by Klaus Hochradel, UMIT Tirol).

## 2.3 Video analysis to determine group sizes

After entering the cave, bats typically flew around for a few seconds or flew to one of two roosting sites, where they stayed for fractions of a second to minutes, and later exited from the cave again. We watched the videos for time periods with flying bats and noted their start and end times and the number of visible bats. We then restricted our analysis to intervals during which the number of visible bats flying inside the cave was constant for at least 10 frames and separated from other bat activity periods by at least 6 frames, referred to as “bat activity periods” (SI NUM). We then checked the synchronized audio recordings of the bat activity periods and excluded all recordings that did contained bat calls other than *R. mehelyi/euryale* calls (see SI NUM).

## 2.4 Acoustic parameter analysis

We only analysed recordings from microphone 1 (Fig. 1), because they appeared to suffer least from reverberance and contained calls of both entering and exiting bats. After high-pass filtering at 70 kHz (2nd order zero-phase Butterworth filter), we used two complementary acoustic approaches to quantify frequency, duration and amplitude parameters of all three components of the echolocation calls (initial FM, CF and terminal FM). In the “individual call analysis”, we measured the acoustic parameters of one echolocation call from each bat activity audio. Individual call analysis directly reveals sensory decisions of individual bats. However, this approach is limited by the difficulty of finding a non-overlapped single call. Particularly in reverberant and multi-bat situations, a biased sampling towards shorter calls that are less likely to be overlapped relative to longer calls may occur. The second approach, the “windowed call analysis” ,therefore complements the individual call analysis by enabling measurements of audio with overlapping calls. We split each bat activity audio into consecutive 50 ms long windows, which could contain multiple and potentially overlapping calls. We then quantified the average acoustic parameters of each window. The windowed call analysis provides average results per time bin, but lacks call-level resolution. Both approaches simultaneously strengthen the interpretation of our results.

### 2.4.1 Individual call analysis

In each bat activity audio, we randomly (see SI NUM) chose one call that was not overlapped by other calls with a signal-to-noise ratio of at least 20 dB (Figure 2.2). We found 226 individual calls across all the bat-activity audio files, which we automatically segmented into their iFM-, tFM- and CF-components (Figure 2.2). We used the *itsfm* package (44) for automatic segmentation of call components based on frequency-time-contours instead of the more commonly used high-/low-pass filtering (16,31,36,45,46) (which does not work well under noisy natural conditions) (44). We defined FM components as those portions of a call where frequency modulation was larger than 2 kHz/ms (see SI NUM for further settings), those with lower modulation as CF-components.

We measured specific parameters for each of the three call components. For the CF-component, we measured peak frequency, received level (using the root-mean-square (RMS))and duration. For the FM-components, we measured the lower frequency (at 10 dB below the level of the FM-component peak frequency), bandwidth (difference between the CF peak frequency and the FM lower frequency), received level and duration. To analyse how bats adjust their call energy between call components (16,31), we calculated the received level difference between the iFM and tFM-components, and the CF-component.

CF-duration in multi-bat contexts showed a non-negligible reduction (4.1). This apparent reduction, however, could originate from a selection bias of our individual call analysis. To eliminate a possible methodological bias, we extended the CF duration analysis to multiple individual calls within each bat activity audio that were used in individual call analysis. We obtained the spectrogram of each bat activity audio and identified a main frequency band within ±1.5 kHz of the average spectrogram peak frequency, which typically contained the CF-components of one bat. In multi-bat recordings with CF-components that were hard to individually assign, we did not include the audio for analysis. We manually set a spectrogram threshold to identify continuous regions in the main band as candidate CF-components, which we manually verified and then calculated their duration (see SI NUM).



**Figure 2: A-B: Individual and windowed call analysis.**

A, B) Spectrogram (A) and oscillogram (B) of a manually selected call for the individual call analysis, with its automatically segmented components: initial frequency-modulated (iFM), central constant-frequency (CF), terminal frequency-modulated (tFM).

C, D) Spectrograms of single-bat (C) and multi-bat (D) recording used for the windowed call analysis, with the 50-ms-long analysis windows indicated.

### 2.4.2 Windowed call analysis

Each bat activity audio was split into consecutive 50 ms windows (Figure 2B, SI NUM). A window duration of 50 ms provided high spectral resolution (20 Hz at 250 kHz sampling rate) to distinguish multiple CF components, and it was about twice the typical call duration and approximately the maximum call duration. To exclude windows without calls or with very faint calls, we only analysed windows whose RMS was at least 20 dB above the maximum RMS of silent windows (see SI NUM). From these windows that contained echolocation calls, we measured each window’s dominant frequencies, FM lower frequencies, and RMS, to complement the corresponding measurements in the individual call analyses. A window’s dominant frequencies are the CF frequencies of all calls in the window and are recognized as local peaks of the smoothed power spectrum with a level of not more than 14 dB below the highest peak (see SI NUM). Dominant frequencies complement the CF peak frequency measurement of individual calls. FM lower frequencies were extracted from each identified FM region in a spectrogram representation of the window (see SI NUM). All spectrogram regions within 70-98 kHz, and above a threshold power were identified as FM regions. The FM lower frequency was the portion of the spectrogram region with the lowest frequency. FM lower frequencies in the windowed analysis correspond to the i/tFM lower frequency of the individual call analysis. The RMS of all samples in a window, describes the average received sound pressure level of the window.

The windowed call analysis does not provide individual-call level data, but a broader characterization of the average call characteristics during single- and multi-bat contexts. Potential changes observed during multi-bat contexts could thus be either an active change in call parameters, but also a side-effect of jointly analyzing the call parameters of multiple bats. We thus created virtual multi-bat activity audio (23, 47), by combining audio-files from single-bat activity audio that were of similar duration (SI NUM), and then performed the windowed call analysis described above on the generated virtual multi-bat activity audio. The virtual multi-bat activity audio generates a null dataset of multiple bats that echolocate together without altering individual call parameters. For all three call parameters, we compared real single-bat, real multi-bat and virtual multi-bat contexts.

Per bat activity audio file, we combined the call parameter measurements obtained from each analysis window into one measure per bat activity audio.

# 2.5 Statistical analysis

## 2.5.1 Individual call analysis

Since the number of recordings with more than one bat was low, we combined all bat activity periods with 2 bats into a multi-bat context and compared call parameters between single- (N=177) and multi-bat contexts (N=49). In the extended CF duration analysis we obtained 328 CF detections from N=97 single-bat activity audio files, and 72 CF detections from N=22 multi-bat activity audio files.

We ran linear mixed-models (LMMs) for each call parameter separately, with the call parameter as response variable, group context (single, multi) as categorical predictor and video-file ID as random intercept, using R 4.0.4 (REF) and the ’lme4’ package [REF]. We initially checked the model fit by performing residual diagnostics, and then estimated model coefficients with a Bayesian approach with non-informative priors (sim function, ‘arm’ package (48)) and report the 95% highest posterior-density compatibility interval (CoI) using the ‘coda’ package [REF], which represents the lower and upper borders of the posterior distribution of the coefficient estimates. Note that compatibility intervals are not equivalent to confidence intervals, even though the numerical values may be similar under certain cases (49). The CoI allows a true probabilistic interpretation that the underlying parameter value falls within a range for the given dataset.

## 2.5.2 Windowed call analysis

To quantify potential change in dominant frequencies, we calculated the range of dominant frequencies for each bat activity audio from the maximum and minimum dominant frequencies across all (). Even in single bat contexts, the recorded dominant frequencies vary because of across any bat activity for two reasons: 1) the effect of the bat’s Doppler shift compensation and 2) the Doppler shift due to the bat’s motion relative to the microphone. These two effects will lead to non-zero dominant frequency range even for single-bat activities (SI NUM).. Since different bat individuals emit different CF frequencies (34), we expect an increased dominant frequency range in virtual multi-bat contexts compared to single-bat contexts. Furthermore, if bats in real multi-bat contexts actively alter their call frequency, we expected an increased dominant frequency range compared to both single-bat and to virtual multi-bat contexts. LMMs were built with dominant frequency range as response variable, group context as fixed effect and recording hour as random intercept (*N*=233, 87, 83 for single, multi, and virtual-multi bat activity audio files).

To understand the theoretically 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 parametrized by the observed data (SI NUM). Briefly we simulated a Doppler-shift compensating bat emitting frequencies between 100-111 kHz, flying past a microphone at various speeds between 1.5-4.5 m/s. The dominant frequency range was calculated as the absolute difference between the frequency recorded by the microphone at the beginning of the flight and the end of the flight. The dominant frequency range estimates from the simulations informed the interpretation of the observed data.

We analysed received level and FM lower frequency across single, multi and virtual-multi activity audio using LMMs for each response variable with similar model structures. In two separate models, received level and lower frequency were response variables. The two models had group context as a fixed variable, along with recording hour and activity audio ID as random intercepts (received level model (single, multi, virtual-multi): N=1753, 1053, 722 windows measured across 233, 87, 83 audio files, lower frequency: 2660, 2927, 1668 measurements over 1427, 963, 654 windows across 231, 87, 83 audio files).

## 2.6 Software

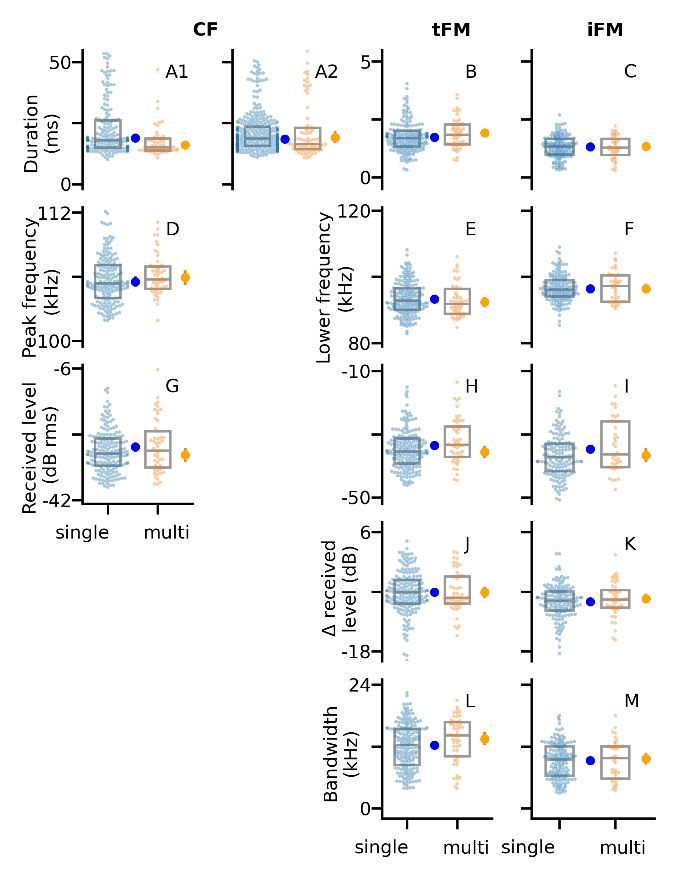
Signal analysis, data manipulation and visualisation were done in Python (50) and its scipy, numpy, matplotlib, soundfile and pandas packages (51–55). Reproducible analysis, documentation and presentation were enabled by the Jupyter Notebook and Rmarkdown projects (56,57). Audio visualisation, preliminary measurements and single call annotations were done with Audacity (58).

# 3 Results

We recorded echolocation and flight behaviour of mixed-species groups of the high-duty cycle bats *Rhinolophus euryale* and *R. mehelyi* as they flew alone and with other bats in a natural cave. The bats performed various flight behaviours in the cave, such as circling, approaches (when two or more bats flew towards each other) and following (one bat behind another) flights. The duration of continuously observed flight bouts varied strongly, ranging from about 0.1 s to 62 s (median: 1.04 s , 95%ile range: 0.5-8.54 s).

In general, the acoustic parameters of individual calls mostly did not differ between single-bat and multi-bat contexts. Likewise, the windowed call-analysis revealed no major differences in received level and FM lower frequency between single-bat and multi-bat and between multi-bat and virtual-multi-bat conditions. In contrast, the dominant-frequency range in the windowed analysis, however, was larger in multi-bat conditions compared to single-bat conditions.

## 3.1 Individual call analysis



**Figure 3: Individual call analysis.**

Acoustic parameters of the constant-frequency (CF), initial frequency-modulated (iFM) and terminal frequency-modulated (tFM) components of individual calls in single-bat and multi-bat contexts (columns). Each row shows a group of related measurements: call duration (**A-C**; **A1**: CF-duration of one individual call per bat flight activity; **A2**: CF-duration of multiple calls per bat flight activity), peak and lower frequency (**D-E**), received level (**G-I**)**J-K)** relative FM-CF received level difference (FM-CF; **J-K**), bandwidth (**L-M**). 177, = 49. Graphs show raw data, box plots (median and quartiles), and the modelled maximum a-posterior estimate (MAP, large dots) with their 95% compatibility intervals (vertical bar; mostly not visible due to narrow range).

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 4.1). Most call parameters showed little or no difference between single-bat and multi-bat observations (Table 4.1) with very small maximum a posteriori (MAP) estimates or compatibility intervals distributed either side of zero. The CF component of multi-bat calls showed slight reduction in duration between -4.45–1.32 ms (95% CoI). However, this apparent reduction in CF duration was not supported by the multi-call extension, indicating no change (Table 4.1 (multi-call extension)) between -1.7-3.02 ms (95% CoI). Multi-bat calls showed a slight decrease in amplitude of upto 0-4 dB in multi-bat calls, and a slight increase in tFM bandwidth of -2.42-0.71 kHz (95% CoI). All remaining had smaller differences between single and multi-bat contexts centered around zero Table 4.1.

**Table 1: LMM results of individual call analysis data showing differences in call parameters between single- and multi-bat contexts****.**

We report the predicted difference and the predicted ratio between the acoustic call parameters in the single- and multi-bat context for the various parameters we measured. The maximum a-posteriori estimate (MAP) is the most likely estimate, and the 95% highest posterior density compatibility intervals (CoI) provide the range of uncertainty in the parameter estimate.

| Measurement | Call component | Difference (Multi-Single) | | | Ratio (Multi/Single) | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | MAP | Lower 95% CoI | Upper 95% CoI | MAP | Lower 95% CoI | Upper 95% CoI |
| Duration (ms) | CF | -2.86 | -4.45 | -1.32 | 0.85 | 0.77 | 0.93 |
|  | CF (multi-call extension) | 0.64 | -1.70 | 3.02 | 1.04 | 0.91 | 1.17 |
|  | tFM | 0.19 | -0.01 | 0.39 | 1.11 | 0.99 | 1.23 |
|  | iFM | 0.02 | -0.16 | 0.19 | 1.02 | 0.88 | 1.15 |
| Peak frequency (kHz) | CF | 0.40 | -0.26 | 1.02 | 1.004 | 0.998 | 1.01 |
| Lower frequency (kHz) | tFM | -0.87 | -2.42 | 0.71 | 0.99 | 0.97 | 1.01 |
|  | iFM | 0.02 | -1.45 | 1.49 | 1 | 0.99 | 1.02 |
| Sound pressure level (dB rms) | CF | -2.16 | -4.09 | -0.22 | - | - | - |
|  | tFM | -2.06 | -4.19 | -0.11 | - | - | - |
|  | iFM | -2.00 | -4.32 | 0.63 | - | - | - |
| SPL difference (dB) | tFM-CF | -0.01 | -1.30 | 1.25 | - | - | - |
|  | iFM-CF | 0.62 | -0.49 | 1.72 | - | - | - |
| Bandwidth (kHz) | tFM | 1.24 | -0.13 | 2.63 | 1.1 | 0.99 | 1.22 |
|  | iFM | 0.38 | -0.90 | 1.62 | 1.04 | 0.9 | 1.18 |

**Table 2:** **LMM results from the windowed call analysis data showing the differences in call parameters between single and multi-bat contexts .**

We report the predicted difference and the predicted ratio between the acoustic call parameters, comparing the single- to the real multi-bat context, and the real multi- to the virtual multi-bat context for the three parameters we measured in the windowed call analysis. The maximum a-posteriori estimate (MAP) is the most likely estimate, and the 95% highest posterior density compatibility intervals (CoI) provide the range of uncertainty in the parameter estimate.

| Measurement | Comparison | Difference (Multi-Single) | | | Ratio (Multi/Single) | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | MAP | Lower 95% CoI | Upper 95% CoI | MAP | Lower 95% CoI | Upper 95% CoI |
| Received SPL (dB RMS) | Multi-Single | 0.20 | -0.40 | 0.90 | - | - | - |
| Lower frequency (kHz) |  | -0.25 | -0.82 | 0.28 | 1 | 0.99 | 1 |
| Dominant frequency range (kHz) |  | 2.14 | 1.74 | 2.62 | 4.91 | 3.48 | 6.48 |
| Received SPL (dB RMS) | Multi-Virtual multi | 0.50 | -0.40 | 1.40 | - | - | - |
| Lower frequency (kHz) |  | -0.41 | -1.20 | 0.37 | 1 | 0.99 | 1 |
| Dominant frequency range (kHz) |  | -0.03 | -0.80 | 0.78 | 1 | 0.71 | 1.29 |

## 

## 3.2 Windowed call analysis

For each window in a bat activity audio we obtained received level and FM lower frequency. For each bat activity audio we also measured the dominant-frequency range.

There was little difference in the received levels and FM lower frequency between multi and single bat contexts (received level: -0.4-0.9 dB 95% CoI, FM lower freq. -0.82-0.28 kHz 95% CoI) (Figure 4.2, Table 4.2).

The mean dominant frequency range (Figure 4.2) was between -0.4 - 0.9 kHz (95% CoI) larger in multi-bat conditions compared to the single-bat condition. The observed difference in dominant frequency range matches the magnitude in simulations when bats do not show any special responses to each other (SI NUM). Received level showed little difference between multi and single bat recordings (-0.4 - 0.9 dB 95% CoI) as well as did FM lower frequency (-0.82 - 0.28 kHz 95% CoI). Compared to single-bat contexts, the dominant frequency range during multi-bat contexts was larger by 1.74 – 2.62 kHz (95% CoI).

We compared the observed multi-bat recordings to virtual-multi bat recordings to estimate if bats were adjusting their echolocation behaviour to the presence of conspecifics. There was little difference in received level and FM lower frequency (received level: -0.4-1.4 dB 95% CoI, FM lower freq. -1.2-0.37 kHz 95% CoI). The difference in dominant frequency range between observed and virtual multi-bat was low as well (-0.8 - 0.78 kHz 95% CoI) (Table 4.2.

All these results taken together suggest bats did not change their echolocation behaviour in the presence of other bats.



**Figure 4: Windowed call analysis.**

Average acoustic parameters of audio recordings in single-bat, real multi-bat and virtual multi-bat contexts (columns) Rows show dominant frequency range of CF-components (**A**), FM lower frequency (**B**), and received SPL (**C**).

Graphs show raw data, boxplots (median and quartiles), and the modelled maximum a-posterior estimates (MAP, large dots) with their 95% compatibility interval CoI (vertical bar; mostly not visible due to narrow interval).

# 4 Discussion

The CF bats have long duration calls that are more likely to suffer from acoustic interference of echoes when in groups. Yet, they are found flying and foraging in cluttered habitats among other conspecifics [pers obs.;(62);(63)]. While many FM bat species have been studied in group flight contexts to alter their echolocation call parameters, studies of group echolocating horseshoe bats are nascent/fewer. One of the reasons for it to be less investigated comes with the technical challenges of analyzing the overlapping signals. Despite the challenge, we quantify the call parameters of echolocating CF bats, when in group by developing/introducing two alternate approaches of extracting information and analyzing the parameters. The first approach used extracts call parameters from identified non-overlapping calls in single and multi-bat activities. Parameters were extracted using the open source itsfm package that segments sounds based on their rate of frequency change, which results in more accurate CF-FM call component segmentation, and thus improved reproducible measurements compared to filtering around the peak frequency (44). The second approach is independent of finding individual non-overlapping sounds but divides the bat activity into successive 50 ms time windows. From each window we measured the overall acoustic parameters without assigning the measurements to individual calls. While coarser in time than the individual call analysis, the window-based approach returns frequency- and level-measurements that are related to individual call parameters and thus complements the individual call analyses. With this, our work presents a useful methodological advance for quantifying overlapping echolocation calls. Results from both these approaches did not support a biologically meaningful difference in echolocation calls with reference to group size for all of the call parameters measured.

ed the overall acoustic parameters of short audio windows without assigning the measurements to individual calls.

## 4.1 CF component

To avoid spectral overlap in groups, the spectral jamming avoidance response (JAR) hypothesis predicts that individual bats in groups will shift their call frequencies away from those of other individuals (25). JAR received mixed support for constant-frequency bats. Several studies in hipposiderid & rhinolophid bats found no changes in CF frequencies (29,39,40,64). In contrast, (24) observed CF frequency shifting in groups of the quasi-CF bat, while (21) found no support in the congeneric *Rhinopoma microphyllum*. Note, however, that *R. hardwickei* is not entirely comparable to the specialized CF-bats of the families Hipposideridae and Rhinolophidae (65), which possess individual-specific acoustic fovea that constrain their echolocation call frequency (33,34).

Our data does not support CF frequency shifting in group echolocation. The spectral jamming avoidance response (JAR) predicts that bats diverge their call frequencies to reduce overlap (25). Compared to single bats, this divergence would lead to an increase in the overall CF frequency range in groups. In our windowed analysis we observed an increase of ~2 kHz in CF frequency range. This observed increase falls within the range of expected values from simulations with no active avoidance responses in them. Variation in flight speed, relative angle to the microphone and inter-individual CF frequency variation can explain the observed increase in dominant frequency range in groups - without any special responses of bats to each other (SI ??). Furthermore, our comparison between observed and virtual multi-bat contexts shows that the CF frequency range observed during real multi-bat contexts does not differ from the CF-peak-frequency range of a random combination of non-reacting bat individuals (virtual multi-bat context). Together, the results suggest that bats that are flying together do not actively change their CF frequencies to reduce or increase overlap.

Our simulations (SI ??) and our recordings of single bats (REFERENCE TO DATA POSSIBLE?) show that a receiver (e.g., a microphone or another bat) in the proximity to a flying CF-FM receives a series of CF frequencies that vary by up to $$3 kHz (Figure ??). This natural variation in received frequency thus decreases the extent of spectral overlap during multi-bat contexts. The combination of individual-specific call frequencies and Doppler-shift driven variation in received CF-peak-frequency makes it unlikely that the CF component would be strongly masked even in groups.

While our individual call analysis suggested a small reduction in multi-bat CF durations by about ms (MAP). This result was not supported by the more robust extended analysis, which showed a negligible difference of ms (MAP) between multi and single bats. We suspect the results from the individual call analysis to be a result of biased sampling as it favoured shorter calls that had a slight advantage in not being overlapped by other calls. Along with CF frequency, *Rhinolophus mehelyi/euryale* do not seem to alter their CF duration too.

## 4.2 FM component

The FM component of CF-FM high duty-cycle bats is likely used for ranging and undergoes large variation as bats approach objects (38). Frequency-changes in group flying FM-bats could indicate a JAR, but could also be a response to the physical presence of other bats in the vicinity (21,29). While not much is known about the iFM-component of CF-FM bats, they do change their tFM-component as they approach objects and during landing (31,36,38). CF-FM bats may thus be expected to respond to conspecifics like FM-bats in groups. (23) Fawcett et al., found that the tFM minimum frequency (-10 dB call peak frequency) decreased by 5 kHz on average in pairs of *Rhinolophus capensis*. In contrast, we only found a decrease of about -0.87 kHz of the tFM lower frequency (-10 dB tFM peak frequency) from the individual call analysis. Our windowed analysis revealed an even smaller decrease of -0.25 kHz in multi-bat calls. Both FM and CF-FM bats also change call duration in the presence of conspecifics and noise (14,16,19,21,23). While we found an increase of tFM duration from single- to multi-bat contexts of 0.19 ms, (23) found an increase of 1.8 ms in pairs, and (16) found a median increase of 0.35 ms in noise compared to calls in silence. Our results are closer to those of (16), while clearly not as strong as (23). FM bats too are known to increase their call durations in the presence of noise (14,19,66), though here too the extent of increase varies across species. While increasing call duration improves echo detection (14,66), the increase in duration we observed here corresponds to about ~10% increase (Table (tab:indcallsummary)), which falls on the lower end of effects seen in FM bats. At least compared to the one other rhinolophid study (23), our effects are small. Whether such small increses in tFM duration lead to biologically relevant improvements in detecting the surroundings in groups remains to be seen.

In contrast to our results, (23) observed an increased tFM duration and bandwidth in *R. capensis* flying in pairs in a novel flight room setting. Potential explanations for this difference might be potential species-differences and the test in a novel versus familiar environment. Since bats possess long-term spatial memory (69,70), the bats in our study might be sufficiently familiar with the cave to tolerate occasional echo masking, particularly in combination with multi-echo integration (68).

## 4.3 Call level

A direct way of improving echo detection is to increase the call level, which both FM bats (14,19,66) and CF-FM bats (16,17,67) regularly do in the presence of experimental playbacks. Because we did not track the 3D-position of the bats in our study, we could not measure their source level and instead analyzed the received level at the microphone. Received levels depend not only on the bat’s source level, but also on the bats’ distance to and calling direction relative to the microphone. Our individual call analysis showed that the received levels of all three call components were ~2 dB lower (MAP) during group flight compared to the single-bat context. In contrast, our windowed call analysis revealed no systematic difference in received level between multi-bat and single-bat contexts and between observed multi-bat and virtual multi-bat contexts.

Despite the observed increase of individually analyzed received levels, there was no change in the windowed analysis, although overlapping calls in multi-bat contexts should lead to a higher received level. We suggest that the similarity in received levels of multi-bat and single-bat windows can be explained by the inequal contribution the nearest bat’s call makes to the received level due to spherical spreading, and the directionality of calls. The fact that multi-bat and virtual-multi bat audio have 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 during group flight showed a drop of around 2 dB that we are unsure how to interpret. This apparent drop in received level could be the result of bats flying further away or emitting more directional calls.

*TB: Not sure how/where to put the points below in…please helppp!!!*

*We expect that 1) the spectral parameters of the CF is less prone to change given that CF-FM bats need to adjust emitted calls to match their acoustic foveal frequency tuning, while the CF duration in multi bats decreases to avoid overlap from other bats calls. 2) While role of iFM is less well understood, the tFM parts of the call can be altered in both spectral and temporal domains, and we expect both the bandwidth and duration to increase in multi bat contexts. The FM parts are less prone to overlap due to their inherently short duration and by altering the parameters can maximize the information encoded in the returning echoes. 3) As for duration of CF or the entire call, we expect that short duration calls will be emitted in multi bat contexts to reduce the possibility of overlap with calls of other bats. (this is not essentially important because if anyways, the CF is not used as part of resolving complexity in multi bat contexts, then the overlap of calls is not important as long as the overlap of the FM is avoided). 4) As a proxy for the measure of change in amplitude, we expect the received levels in multi-bat contexts to reduce in multi-bat contexts in an echoic natural cave and also presence other bats very close to one another.*

[DON’T HAVE A SEPARATE “OUTLOOK” section, on the same level as INTRO/METHODS/RESULTS/DISCUSSION. The journal won’t let you have it anyway; also this section is not so important to warrant a separate high-level section.

Use subheadings in the discussion, if you like.

Also, this section is too long. Try to condense it to one (or two) final paragraphs that provide a conclusion and outlook. If there are still details, the belong to the previous sections. Here, you want to provide a concise statement outlining the general scientific ideas, results and ways forward]

Besides changes in temporal, spectral and amplitude parameters on the level of individual calls, some of which we analyzed in this study, bats also change parameters on the level of call sequence, such as call intervals and duty cycle (14,15). In contrast to single-bat contexts, measuring call intervals is challenging in multi-bat recordings due to difficulties in assigning calls to individuals and temporal overlap between multiple calls and echoes.

Despite bats’ outstanding flexibility in adjusting to ss , we found no obvious change in call parameters in free-flying CF-bats in small groups of up to four bats. This strongly suggests that free-flying CF-bats do not suffer from sensory problems when flying in small groups, even in reverberant environments. We propose that multiple reasons can explain why such situations are not very challenging, and why bats thus do not alter their calls.What are the possible explanations for the absence of a strong echolocation response in groups? Our data suggests that echolocation in groups with a few bats (2-4) bats may not be very challenging for multiple reasons. CF-FM bats rely use on the tFM component to detect the distance of objects around them for object ranging (31). The tFM components are short ($\leq$3ms, 95 percentile value), and likely emitted about every 40-50 ms which is equivalent to a tFM duty cycle between 6-7.5%. When two bats fly togetherFor a pair of bats at these duty cycles, the probability that the tFM-component of one bat overlaps the other bat’s tFM-echo of one tFM echo being overlapped by another bat’s tFM call component is only relatively low at most between up to 1.6 - 2.1% (see SI 0.10 for calculations). 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. Modelling showed that FM- bats can detect all of their echoes in small groups of up to 10 individualsare unlikely to face major detriments to their echolocation (28). FM bats integrate echoes across multiple calls and are thus resistant to occasional disruptions in echo arrival (68). We suggest that the same resistance to jamming should also apply in CF-FM bats using the FM component for ranging, explaining why the horseshoe bats here did not show call change their calls during group flights from solitary echolocation.

In contrast to our results, (23) observed an increased tFM duration and bandwidth in *R. capensis* flying in pairs in a novel flight room setting. Potential explanations for this difference might be potential species-differences and the test in a novel versus familiar environment. Since bats possess long-term spatial memory (69,70), the bats in our study might be sufficiently familiar with the cave to tolerate occasional echo masking, particularly in combination with multi-echo integration (68).

In our opinion, the primary obstacle to furthering studies in group echolocation is technical, especially in analysing overlapping sounds. Here, we presented a series of workflows such as the windowed call analysis and measurement of CF durations in multi-bat contexts. To improve the reliability of call component measurement, we also developed the itsfm toolkit to segment call-components. Further work still remains to be done, as highlighted above, in the development of call-identity assignment when there are multiple overlapping calls recorded under reverberant conditions.

**4.x Conclusions**

Despite bats’ outstanding flexibility in adjusting call parameters to tasks and contexts to optimize sensory information, we found no obvious change in call parameters in free-flying CF-bats in small groups of up to four bats. This strongly suggests that free-flying CF-bats do not suffer from sensory problems when flying in small groups, even in reverberant environments. Our results add to the growing body of literature (21,22,40) showing that echolocation in (small) groups is not so special after all and can be solved by the bats’ general repertoire of sensory strategies for dealing with sensory challenges. While bats do indeed alter their echolocation behaviour in the face of sensory challenge in groups, it is important to consider that not all types of group-situations will lead to the same type of sensory challenge. Our results thus match the increasing evidence that jamming does not pose a problem for FM-bats (14,21,22,28,41) now extending this to high-duty cycle CF bats. 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. To also advance the understanding of group echolocation, which is often an egocentric perspective, it would be interesting to record and measure calls in the field with on board microphones in freely behaving bats.

# Data and code availability

All data and code used process data and generate the results and figures in the paper are available at the following Github repository: <https://github.com/thejasvibr/mhbc-online/> and the Zenodo link *INSERT ZENODO LINK HERE*

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# Author Contributions

Author contributions in alphabetical order. 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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