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Spatial differences in soundscape for bats on the edge versus the center of a bat swarm

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Previous work has indicated that bats use harmonic structure to identify target echoes from background clutter. Although advantageous for detecting the presence of targets straight ahead, the question remains as to how bats modify echolocation, if at all, when identifying the presence and distance of objects in the periphery, which might be needed in dense group flights. Building on this premise, we predicted that free-tailed bats in central positions of swarms, in a tight cluster of acoustic clutter, use different echolocation signals than bats on the periphery. We investigated this by quantifying the soundscape via synchronized audio and visual analysis, focusing on spatial positioning. To overcome the challenge of recording inside a dense swarm, we developed a microphone/camera unit carried by a trained Harris's hawk that flew through the bat swarm. Frequency spectra were extracted and analyzed as a function of the position in the swarm. We found a significant difference in the soundscape between the edge and center of the swarm for frequencies above 40 kHz, suggesting bats in central positions of the swarm produce echolocation signals with more energy in higher frequencies, which may aid in the sorting efficiency of their own call's echoes from conspecifics.

1. INTRODUCTION

Many species of bats form large aggregations at roosts that can contain millions of individuals, facilitating a highly social lifestyle (Dechmann, Kranstauber et al., 2010). Their social life includes social grooming, shared parental care, and cooperative hunting (Wilkinson et al., 2016). All these behaviors suggest that bats have very close social bonds within their colonies and have evolved mechanisms to overcome the challenges of living in such dense aggregations.

By emitting high-frequency vocal signals that reflect off objects and surfaces and processing the returning echoes, bats craft a representation of their surroundings (Simmons and Stein, 1980; Corcoran, Moss, 2017; Jones & Holderied, 2007; Boonman, Parsons, Jones, 2003; Boonman, Bar-On, Yovel, 2013). This task becomes even more challenging for bats flying in groups, as an individual must navigate an area without colliding with thousands of conspecifics moving in the same space. Some bats have developed adaptive behaviors to avoid each other while flying in a dense swarm (Ulanovsky and Moss, 2008; Lin, Abaid, and Müller, 2016), including acoustic modifications (Amichai, Blumrosen, Yovel, 2015; Takahashi et al., 2014; Ratcliffe et al., 2004). Yet, these dynamic mechanisms have yet to be studied in very dense aggregations of their natural environment.

Previous studies have indicated that bats alter the parameters of their echolocation calls based on their environment and task demands (McGowan & Kloepper, 2020; Falk et al., 2014; Sulykke & Moss, 2000). McGowan & Kloepper's (2020) work highlights the prevalence of long-duration, narrow-bandwidth echolocation calls in open environments, while cluttered environments tended to feature broadband short-duration calls. Long-duration narrowband calls are particularly well-suited for open spaces due to their heightened long-range detectability and the reduced sensory information needed to navigate effectively in such environments (McGowan & Kloepper, 2020). However, shifting to an acoustically complex area presents a more challenging sensing task, with a high amount of echoes returning from non-target objects (Warnecke et al., 2015). Under these conditions, short broadband calls may provide a higher resolution of the environment (Falk et al., 2014; McGowan & Kloepper, 2020; Moss et al., 2011). Furthermore, Siemers & Schnitzler's (2004) research indicates that bats emitting shorter, broadband signals are well suited to approach cluttered environments. This leads us to believe that they may be adjusting their calls to the demands of flying in dense groups.

This study investigates the potential for bats to use different echolocation signals when flying in a group depending on spatial position and sensory challenge. The focal species in this study, the Brazilian free-tailed bat (*Tadarida brasiliensis*), forms some of the largest known animal aggregations (Kloepper et al., 2016) and emits a common type of echolocation signal referred to as a frequency-modulated (FM) call (Simmons et al., 1978; Ratcliffe et al., 2004). Because bats produce different call types depending on the clutter in their environment, we predicted that we would find different characteristics in the overall soundscape depending on whether bats were at the periphery of the swarm, in which clutter was reduced, versus in the center of the swarm, when clutter was highest.

2. METHODOLOGY

For this project, we collected video and audio data from the bats at a cave in Sierra County, New Mexico, using a mobile falconry platform. A trained Harris's Hawk flew through swarms of Brazilian free-tailed bats during peak emergence times, when bats were leaving their cave to go hunt. We flew the hawk from one side of the swarm to the other (Figure 1). The hawk carried a customized

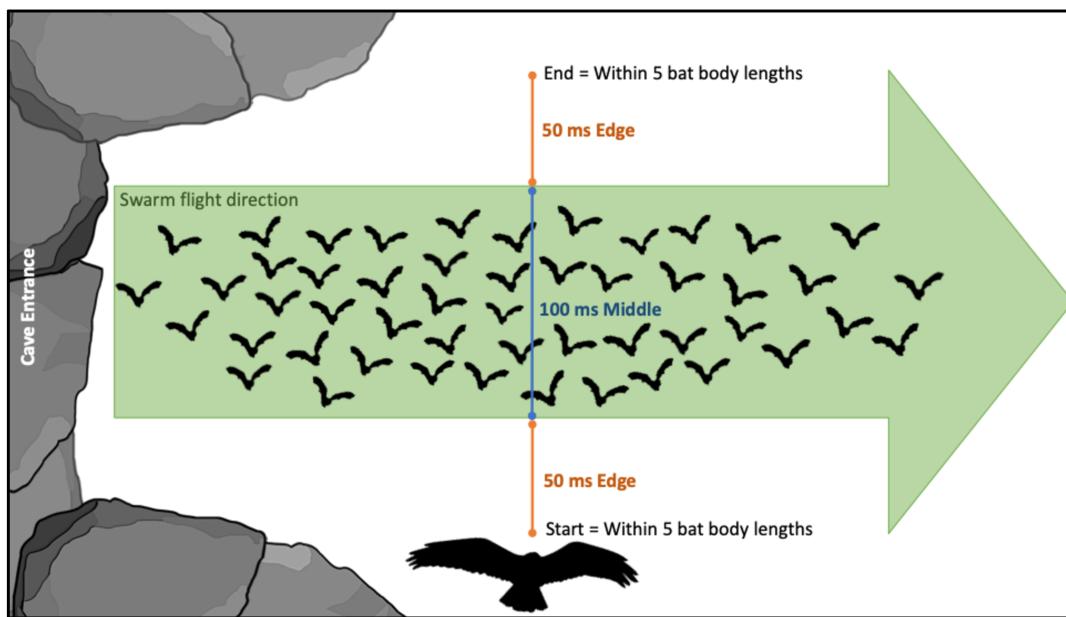


Figure 1: Illustration of the determination of “edge” versus “middle” conditions. If the hawk was more than 5 bat body lengths (50 cm) away from the nearest bat, it was on the Edge. While if the hawk was less than 5 bat body lengths from the nearest bat, then it was in the middle.

microphone (containing a Knowles SiSonic MEMS microphone with flat frequency response between 10 and 100 kHz) and camera unit to collect visual and audio data (Figure 2). Additional cameras positioned around the cave entrance to capture multiple perspectives of the swarm.



Figure 2: The microphone and camera unit that the hawk carried to collect data as she flew through the bat swarm are located on the hawk’s head and upper back.

The video and audio data were synced using an auditory and visual cue (i.e., a sequence of claps), and singular passes were extracted to analyze them individually. We selected passes of the hawk through the swarm based on how close the hawk was to the outermost bat in the swarm (Figure 2). We defined the start of a pass when the hawk was approximately within 50 cm of the nearest bat, as judged from the video images. If the hawk did not approach the swarm within 50 cm, then the pass was not included in the analysis. The relative position of the hawk and bats was determined by the combination of onboard visual data and the additional monitoring cameras positioned around the cave entrance. The end of a pass was determined by the same principle as the starting point after the hawk had flown through the swarm's center.

Audacity was used in order to view and assess the structural shifts that occurred between echolocation pulses and overall echolocation structure. In each file we applied a high pass filter of 10kHz to our acoustic recordings before analysis. The audio files were then split into middle, left and right in accordance with the orientation of the videos. The left and right sections were 50 ms each, while the middle was taken from the 100 ms center section of the audio file (when the hawk was in the center of the swarm). From these three splits, a frequency spectra plot was created from each orientation. To quantify the data, the frequency and amplitude values were exported into an excel sheet based on pass number and position. To normalize the values, we subtracted the maximum amplitude from all amplitude values in a singular pass and repeated for all passes. The data were then exported into R for further analysis.

To perform statistics, the normalized data was separated by each condition (edge and middle) into eight different bins based on frequency. Each section represented a 10 kHz segment from 20-100 kHz. The average amplitudes were calculated for all frequency bins and each condition to allow for the comparison of amplitude over different frequencies. A paired t-test was performed for each segment to test whether there was a difference between the calls on the edge and middle of the swarm.

3. RESULTS

A total of 23 passes were used in our analysis to detect any differences in location. We first performed a t-test was to detect any significant difference in the values between the left and right edges, finding that they were similar we combined both into a single “edge” condition and compared it to the middle. After running paired t-tests, seven out of the eight frequency bins resulted in statistically significant differences between the edge and middle of the swarm. The frequency bin from 30-40 kHz was the individual section that was not significant, which aligns with the common frequency range that they echolocate in (Tressler & Smotherman, 2009). Frequencies above 40 kHz showed an increase in the amplitude difference between the edge and the middle conditions (Figure 3). The relative amplitude of the middle was higher than the edge in all frequencies (Figure 4).

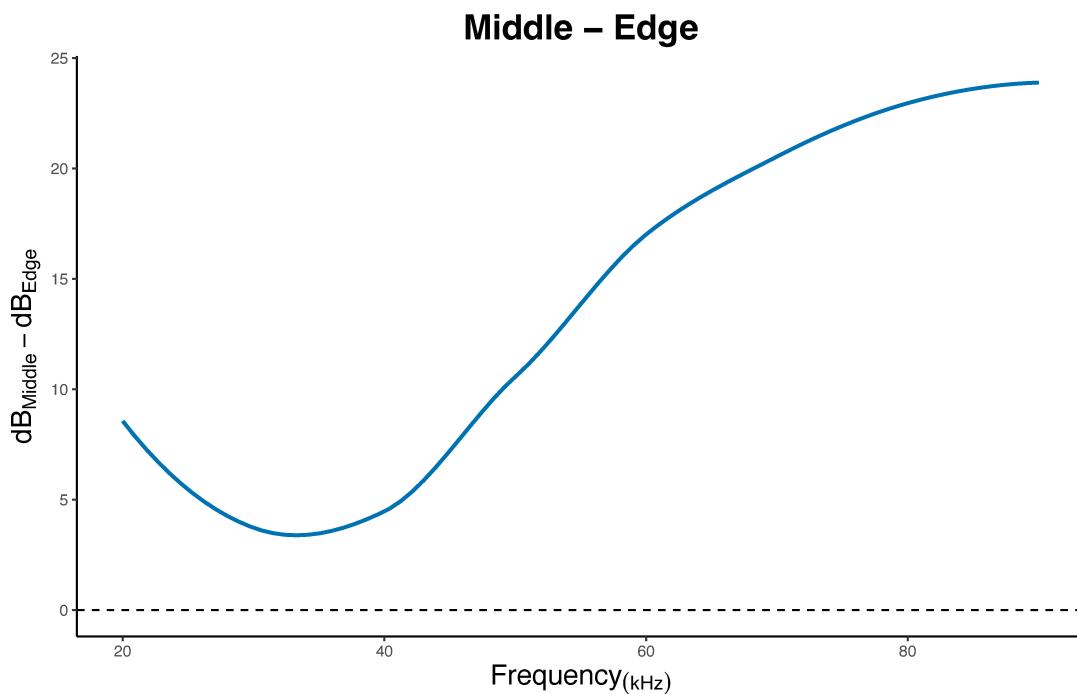


Figure 3: Average difference between the Middle and Edge (dB) conditions as a function of frequency (kHz) across all passes.

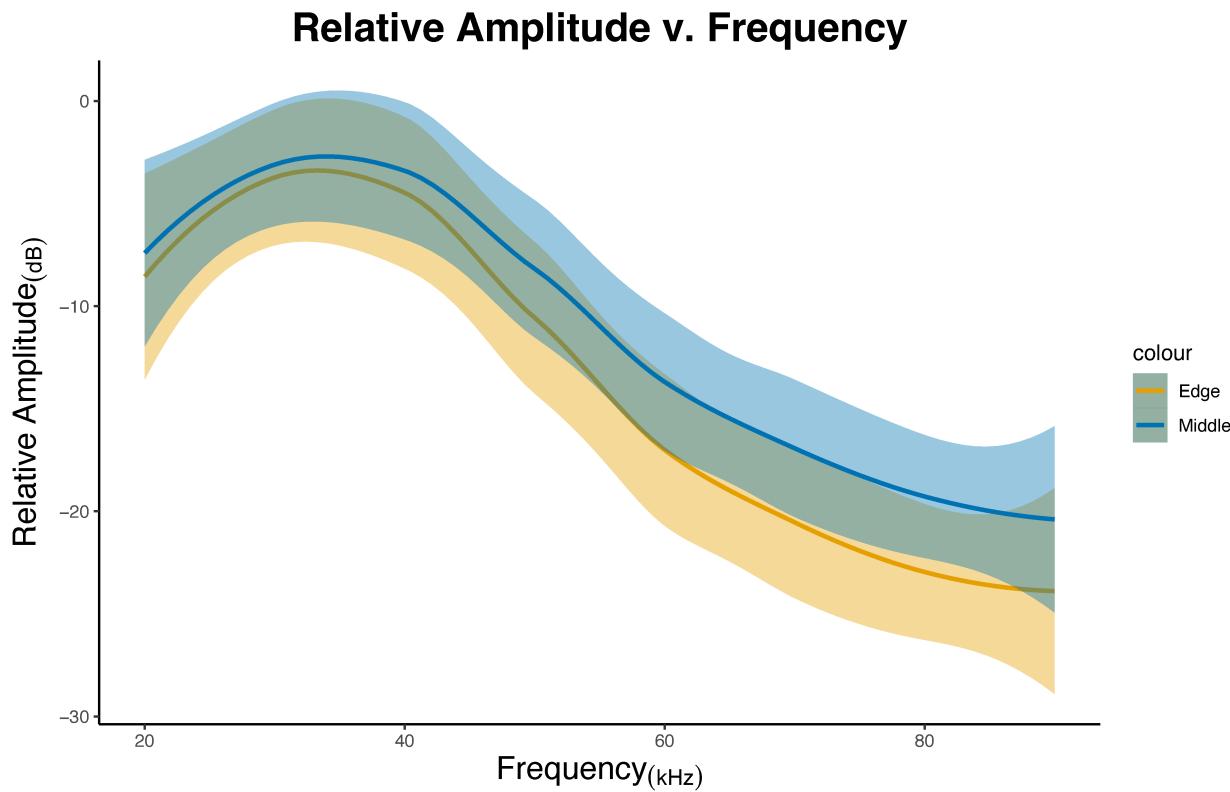


Figure 4: Relative amplitude (dB) as a function of frequency (kHz) in terms of the two conditions (Middle and Edge). The solid line represents the average across all passes, and the shading represents the standard error for the edge (yellow) and middle (blue) condition.

4. CONCLUSIONS

These results suggest that the bats in the middle of dense swarms shift the relative energy of their echolocation calls compared to bats at the periphery of the swarm (Figure 4), resulting in a greater proportion of energy at higher frequencies for bats in the middle versus the edge of the swarm. This may be a strategy to distinguish their own calls' echoes from a conspecifics', as bats rely on higher frequency information to detect a call and suppress off-axis echoes (Bates et. al., 2011). This gives insight into the bigger picture of how bats in swarms may avoid conspecifics through echolocation. By utilizing this shift in call frequency, bats can sort their own echoes from the surrounding clutter with higher efficiency (Moss et. al., 2011). At an individual level, this adaptive frequency alternation phenomenon might play a role in the overall coordination of group movement (Demartsev et al., 2023). This coordination is further strengthened by the frequently observed but less commonly documented parallels between bat flight patterns and those of birds.

It is possible, however, that the results found in this study were influenced by other factors. The attenuation of higher frequency sound may have had an effect on this data (Bates, Simmons, Zorikov, 2011). However, we made an effort to control for these effects by averaging as the bat moved through the swarm, which should aid to control for variation from bat to bat. The observed similarity in both edge data sets implies that the spatial relationship between the hawk and the bats did not substantively contribute to the findings. Future work with multiple microphones could allow for acoustic localization to further investigate whether the changes in soundscape reflect true changes in acoustic behavior by bats based on position in the swarm.

While this study sheds light on how the swarms' soundscapes are shifting and suggests that bats are changing their echolocation behavior in order to distinguish from their conspecifics, there are still avenues that we anticipate future studies will explore. Confirmation that the individuals are modifying their emission frequency is necessary in future studies that tag individuals within a swarm or use acoustic localization. Exploring other parameters of their echolocation (i.e., intensity, duration, bandwidth, etc.) could also prove to be beneficial in revealing the mechanisms that they employ in dense acoustic environments.

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