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Echolocation adaptations during high-speed roost re-entry for Brazilian free-tailed bats (*Tadarida brasiliensis*)

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Abstract: Some bats re-enter their cave while using echolocation at very high speeds, but this behavior is poorly studied. Thermal imaging and an array of ultrasonic microphones were used to investigate the acoustic adaptations made during high-speed re-entry for single bats entering a cave. There was a significant overall effect between bat, distance to the ground, and its flight speed on pulse duration and interpulse interval (IPI). The data imply that overall bats reduce pulse duration, IPI, and bandwidth as they approach the cave and slow down, but the behavior changes among individuals.

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1. Introduction

Bats use echolocation to orient themselves and locate prey, and modify their echolocation calls during foraging or when bats fly from open to cluttered environments (Neuweiler, 2000). Brazilian free-tailed bats (*Tadarida brasiliensis*) are known to have one of the most flexible echolocation systems among bat species (Simmons *et al.*, 1978), changing their calls during emergence (Gillam *et al.*, 2010) and foraging (Gillam and McCracken, 2007); however, little is known about the echolocation calls of these bats, or any bat species, when individuals re-enter the roost. When returning to their roosts, Brazilian free-tailed bats fly at very high altitudes (Williams *et al.*, 1973), at a close proximity to conspecifics (Wilkins, 1989), and up to speeds of 128 km/h (Davis *et al.*, 1962). Furthermore, in some situations individuals fly perpendicular to the ground, making a sharp 90° turn to enter the cave (Kloepper, 2018).

One of the challenges for bats echolocating during such high-speed flight is the Doppler effect, which causes the echolocation calls of bats to increase in frequency and become compressed as they are flying in the air, resulting in ranging errors (Boonman *et al.*, 2003; Holderied *et al.*, 2006). Constant-frequency bats actively compensate for Doppler shift by reducing the frequency of emitted calls during flight to maintain a constant receive echo (Schnitzler, 1973). Frequency-modulated (FM) bats, however, may rely on the Doppler tolerance of the FM signal to avoid ranging errors (Boonman *et al.*, 2003), or may reduce the duration and increase the bandwidth of FM pulses when approaching obstacles (Holderied *et al.*, 2006). These changes may be more pronounced in the fast flying free-tailed bats, yet no studies have been conducted to investigate how individuals adapt their calls during roost re-entry.

In this study, we examine the acoustic adaptations made during high-speed re-entry of individual Brazilian free-tailed bats to determine how distance to the ground and flight speed affect their FM calls. Specifically, we test the hypothesis that call duration and interpulse interval (IPI) will decrease and bandwidth will increase as the bats approach the ground, and that this relationship may be further influenced by flight speed. Our results represent the first characterization of the re-entry behavior of individual bats as they return to their cave.

2. Materials and methods

Acoustic and thermal data were collected between July 30 and August 2, 2016, at a gypsum cave in Barber County, Oklahoma. Two Wildlife Acoustics SM3 Bat audio recorders (Wildlife Acoustics, Inc., Maynard, MA) (sample rate 256 kHz, 0 dB gain) were synchronized, and a *y*-shaped array of four Wildlife Acoustics SMM-U1 microphones (Wildlife Acoustics, Inc., Maynard, MA) (omnidirectional, Fig. S1 in Supplementary

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Material[1] for frequency response) was arranged at the entrance of the cave opening (Fig. 1). Prior to data collection, the microphones were calibrated and found to be within 1 dB of each other. Each microphone was laser measured to be exactly 2 m away from each other, with 120° between each microphone. Because the two recording units were separate and synchronized manually, we did not achieve the synchronization precision necessary to perform acoustic localization of individual bats. Rather, the array recording was used to identify the loudest acoustic signal for each echolocation pulse. To obtain localization information for the bats, a FLIR a8300sc thermal imaging camera was positioned facing the cave opening and pointing up toward the sky, to track the bats as they approached the cave roost. Since solo bats at this recording location return to the cave in nearly linear paths, perpendicular to the ground (Kloepper, 2018), the position of our thermal camera allowed for close approximation of the bat's true flight path. The microphone array was manually synchronized to the FLIR camera. We recorded audio at 256 kHz and thermal imagery at 120 frames per second.

The thermal videos were viewed in QuickTime Player 7 version 7.6.6. We determined, via thermal imagery, the periods where isolated bats were approaching the cave. The trajectory of each bat's flight was traced as it re-entered the cave via a customized algorithm in MATLAB, providing an *x*, *y* coordinate for each video frame as the

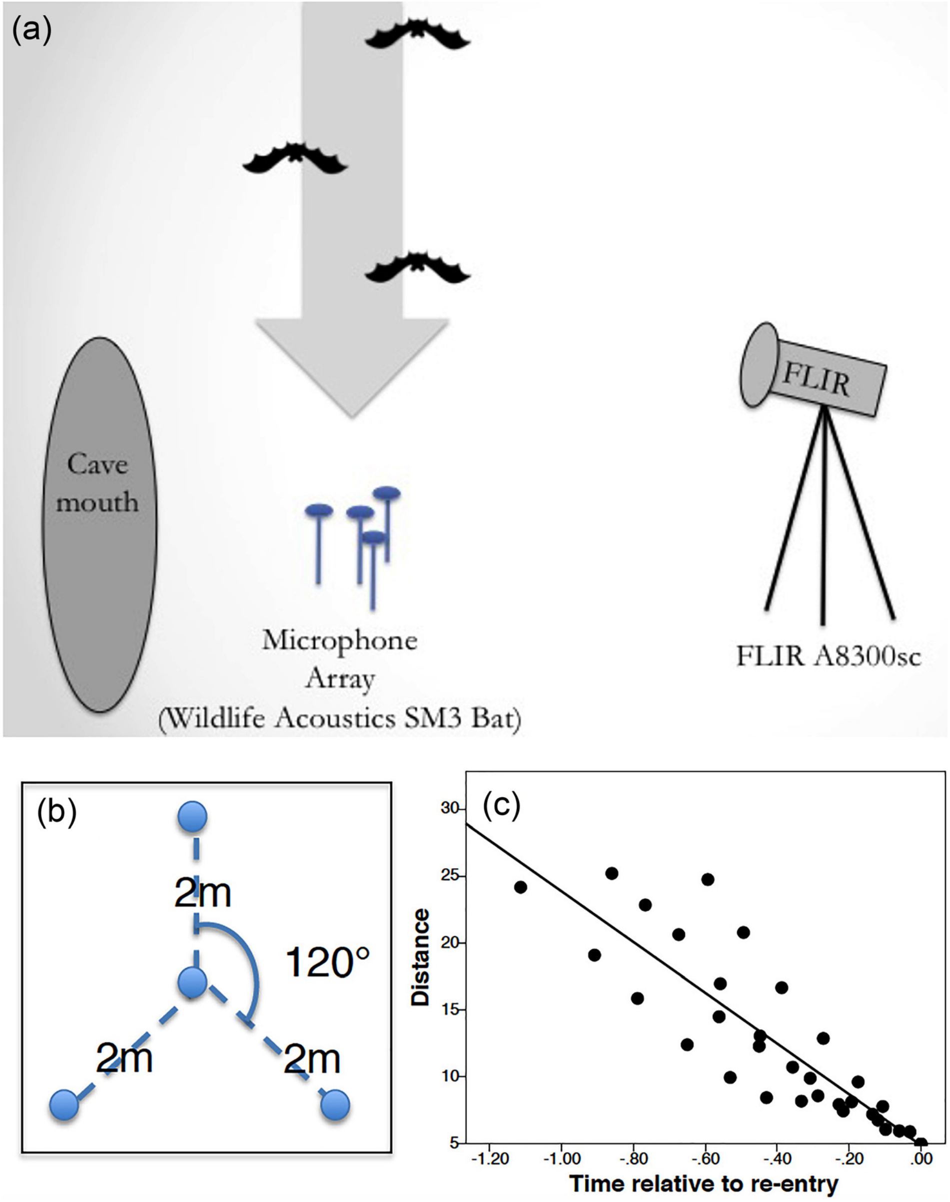

Fig. 1. (Color online) Diagram of the experimental set-up. (a) The microphone array and thermal imaging camera set-up outside of a gypsum in Barber County, Oklahoma, (b) the arrangement of the microphones in the array, and (c) the correlation between time relative to the maximum amplitude signal (determined from audio) and distance from ground (determined from thermal video) ($r = -0.880$, $n = 35$, $p = 0.001$).

bats approached the cave. From these values, we determined the distance, in pixels, the bat traveled over time. To convert from pixels to meters, we determined the vertical field of view of the thermal camera by combining the manufacturer lens field of view (degrees) and then correcting for the distance the thermal camera was from the cave. This resulted in a pixel-meter conversion value. Due to the high data rate of the thermal camera, many bat videos froze for multiple frames, preventing precise bat localization. These videos were eliminated from the dataset. Speed and distance parameters were calculated from the remaining videos.

For the audio recordings, audio files were aligned to correspond with the thermal video files. Due to video frame drift and freezing within our video files, we had a ±0.5 s uncertainty in the alignment of our video and audio files. Therefore, we aligned our thermal video and acoustic data under the assumption that the highest amplitude signal received by our acoustic recordings was produced by the bat at its closest distance to the ground. For some bats that had clear videos, the acoustic files contained high-frequency insect noise that masked the echolocation signals of the bats, preventing acoustic analysis. For the remaining, "good" files, we performed a Doppler and atmospheric absorption correction using the distance and speed metrics calculated from the thermal videos (Boonman and Jones, 2002; Holderied *et al.*, 2006). The acoustic parameters of our corrected pulses were calculated using a customized algorithm in the MATLAB environment based on the loudest pulse recorded on the array. For each pulse we determined the time the pulse was emitted, the −20 dB bandwidth, the duration, and the IPI. The time each pulse was emitted was standardized relative to the maximum amplitude signal received by the microphones. To investigate the acoustic adaptations during re-entry, we examined the effect of bat, distance to the ground, and flight speed on pulse bandwidth, duration, and IPI using multiple linear regression. All statistics were performed and analyzed in IBM SPSS v. 23.

3. Results

Across our four recording mornings, we extracted 18 single-bat re-entry files. After removing bats where the thermal videos froze or the acoustic files were unusable due to high frequency insect noise, we obtained a final sample size of 4 bats and 35 pulses to work with in our data analysis. The flight speed over return distance, as determined from the thermal imagery, is shown in Fig. 2. Faster flight speeds were recorded at greater distances from the cave, with the maximum recorded flight speed of 44 m/s, and all bats reduced speed as they returned to the roost, with the minimum recorded flight speed of 4 m/s. The time relative to the maximum amplitude signal (determined from the acoustic recordings) and distance from the ground (determined from thermal imagery) were strongly correlated [$r = -0.880$, $n = 35$, $p = 0.001$, Fig. 1(c)]. An example sequence of pulses during re-entry is depicted in Fig. 3. At distances away from the cave [Fig. 3(a)], bats produce signals that are 10–15 ms in duration. As the pulses progress during re-entry [maximum amplitude signal, Fig. 3(i)], pulse durations shorten to approximately 5 ms.

Results of the multiple linear regression indicated an overall significant effect between bat, distance to ground, and speed on pulse duration [$F(3,31) = 20.241$, $p < 0.001$; adjusted $R^2 = 0.629$]. Individually, pulse durations significantly decreased as bats approached the cave ($\beta = -0.286$, $p < 0.001$; Fig. 4(a) and pulse durations decreased with decreasing flight speed [$\beta = -0.121$; $p = 0.005$; Fig. 4(d)]. The mean

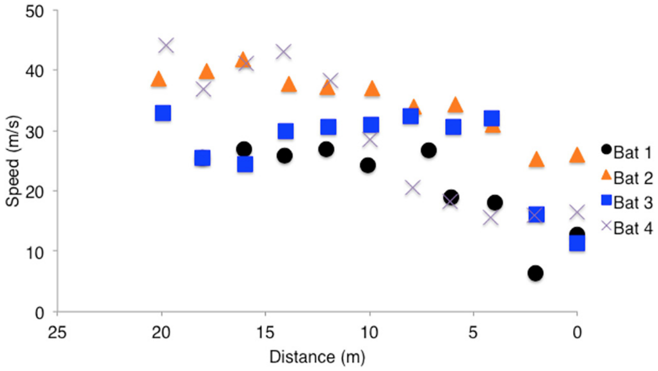

Fig. 2. (Color online) The speed (m/s) of bats as they approached the cave opening. Speed and distance were determined from thermal imagery (see Sec. 2).

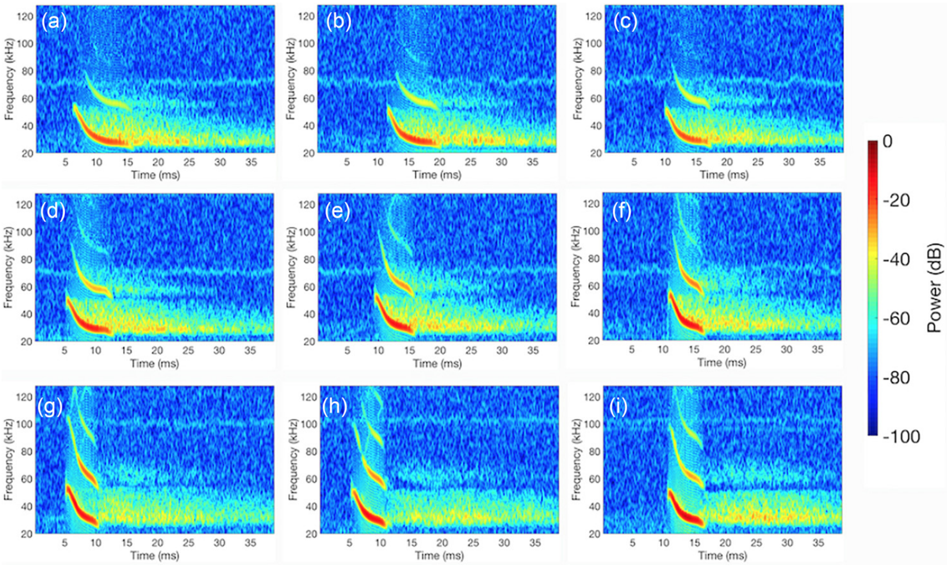

Fig. 3. (Color online) Example spectrograms of a sequence of re-entry calls [(a)–(i)] for an individual bat returning to the cave.

pulse duration was also significantly different among individual bats ($p < 0.001$). There was also an overall significant effect between bat, distance to the ground, and speed on IPI [$F(3,31) = 8.997$, $p < 0.001$; adjusted $R^2 = 0.414$]. IPIs significantly decreased as bats approached the cave [$\beta = -0.004$, $p < 0.001$; Fig. 4(b)], but there was no significant effect of speed or bat individually on IPI [$p > 0.05$; Fig. 4(e)]. Pulse bandwidth was also significantly affected by distance, speed, and bat overall [$F(3,31) = 4.354$, $p = 0.011$; adjusted $R^2 = 0.228$; Fig. 4(c)]. Individually, bandwidth significantly increased as bats approached the cave [$\beta = 0.317$, $p = 0.036$; Fig. 4(c)] and increased with increasing flight speed ($\beta = 0.220$, $p = 0.032$). Despite inconsistent patterns among bats, there was no individual significant effect of bat on pulse bandwidth ($p > 0.05$).

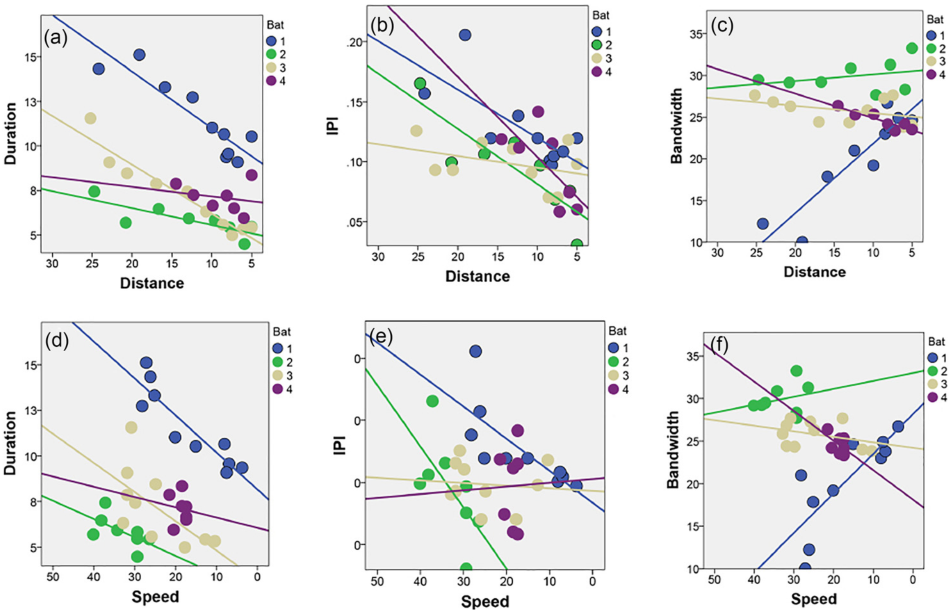

Fig. 4. (Color online) The relationship between (a) distance from cave (m) and duration (ms) for each bat (Bat 1 $R^2 = 0.814$, Bat 2 $R^2 = 0.647$, Bat 3 $R^2 = 0.919$, Bat 4 $R^2 = 0.050$), (b) distance from cave (m) and IPI (ms) for each bat (Bat 1 $R^2 = 0.560$, Bat 2 $R^2 = 0.722$, Bat 3 $R^2 = 0.140$, Bat 4 $R^2 = 0.501$), (c) distance from cave (m) and bandwidth (kHz) for each bat (Bat 1 $R^2 = 0.837$, Bat 2 $R^2 = 0.098$, Bat 3 $R^2 = 0.170$, Bat 4 $R^2 = 0.842$), (d) speed during re-entry (km/h) and duration (ms) for each bat (Bat 1 $R^2 = 0.823$, Bat 2 $R^2 = 0.355$, Bat 3 $R^2 = 0.407$, Bat 4 $R^2 = 0.013$), (e) speed during re-entry (km/h) and IPI (ms) for each bat (Bat 1 $R^2 = 0.569$, Bat 2 $R^2 = 0.403$, Bat 3 $R^2 = 0.009$, Bat 4 $R^2 = 2.356 \times 10^{-4}$, and (f) speed during re-entry (km/h) and bandwidth (kHz) for each bat (Bat 1 $R^2 = 0.652$, Bat 2 $R^2 = 0.069$, Bat 3 $R^2 = 0.122$, Bat 4 $R^2 = 0.267$).

4. Discussion

Our results provide initial data to understand how bats adjust echolocation during high-speed roost re-entry. As bats return to the roost and approach the cave opening, they reduce their flight speed (Fig. 2). This change in flight behavior occurs concurrently with a change in echolocation behavior: overall, bats reduce pulse durations, shorten IPIs, and increase pulse bandwidth as they approach the cave opening and slow down (Fig. 4). These acoustic adaptations, however, are not driven solely by distance to the ground, as speed further influences call characteristics, with bats shortening call duration and increasing bandwidth at faster flight speeds. These changes we report on call parameters during re-entry are further evident in close inspection of the pulse spectrograms (Fig. 3).

Bats produce similar FM changes when shifting from search to approach phases during foraging, in which bats produce more rapid calls with wider bandwidths for exact target localization (Schnitzler and Kalko, 2001) or in cluttered environments, where bats need to avoid obstacles (Schnitzler *et al.*, 1987). Bats also produce similar FM changes when approaching obstacles (Holderied *et al.*, 2006). During re-entry, we found bats flying in excess of 44 m/s (158 km/h; Fig. 2) straight toward the ground. At these speeds, the bats would need precise information about the ground and/or cave opening to avoid collisions with the ground and coordinate the sharp turn to enter the cave. Increasing pulse bandwidth and producing shorter, more rapid calls during close re-entry could aid in the bat's precise localization of the ground and cave opening to minimize ranging errors.

Bats demonstrate individual variation in echolocation behavior (Obrist, 1995) and we found similar results with our data. The results depicted in Fig. 4 suggest that although there is variation among echolocation behavior in individuals, overall bats demonstrate the same strategy of reducing pulse durations and IPIs as they approach the cave and/or slow down. It is important to note that not all bats demonstrate the same relationship in bandwidth across flight speeds or cave distances [Figs. 4(c) and 4(f)], with one bat increasing pulse bandwidth as it approached the cave and slowed down. Due to our experimental design, we cannot ensure the array captured a true on-axis signal, which would reflect the full spectral components of the call. Instead, we can only ensure that we analyzed the loudest amplitude signal recorded by our array. Therefore, we suggest that the bandwidth results be taken with caution.

One of the limitations with our study was the uncertainty in the synchronization of our acoustic and video recordings. Due to this, we used the assumption that the loudest call received by our array was produced when the bat was closest to the ground in order to align our audio and video. The strong correlation between the distance of the bat (determined by video) and time of each pulse relative to re-entry [Fig. 1(c)] indicates that the bats are steadily getting closer to the cave as they produce echolocation signals, and that our use of video for distance was likely a good approximation in lieu of precise acoustic localization. Future studies, however, should utilize more precise three-dimensional (3D) localization, whether it be from acoustic localization or stereo video, to accurately link flight and acoustic behavior during re-entry.

The results of this study provide the first insight into the acoustic adaptations made by bats during high-speed, vertical flight during cave re-entry. We found that bats returning to their roost fly in excess of 44 m/s. As they approach the ground and roost opening, bats shorten pulse durations, increase pulse bandwidths, and produce pulses with shorter IPIs. These acoustic adaptations likely enable precise localization needed to coordinate flight behavior into the roost at high speeds. Future studies investigating these bats during re-entry using larger sample sizes and precise 3D localization, or when flying in groups, can further elucidate acoustic and flight adaptations made during complex high-speed flight for echolocating bats.

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[1] See supplementary material at https://doi.org/10.1121/1.5085308 for the frequency response in the y-shaped array of four Wildlife Acoustics SMM-U1 microphones.

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