Echolocation behavior of Brazilian free-tailed bats during dense emergence flights

Erin H. Gillam,* Nickolay I. Hristov, Thomas H. Kunz, and Gary F. McCracken

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, USA (EHG, GFM)
Center for Ecology and Conservation Biology, Boston University, Boston, MA 02215, USA (NIH, THK)
Present address of EHG: Department of Biological Sciences, North Dakota State University, Fargo, ND 58108-6050, USA
Present address of NIH: Department of Life Sciences, Winston-Salem State University, Winston-Salem, NC 27110, USA

* Correspondent: erin.gillam@ndsu.edu

Brazilian free-tailed bats (*Tadarida brasiliensis*) emerge from cave roosts in dense columns in which adjacent bats are separated by only small distances. We describe and quantify variation in the structure of echolocation calls produced by these emerging bats and determine if call structure changes in relation to the rate of emergence measured using thermal infrared imaging. We recorded emergence calls at 2 roosts, 1 housing approximately 200,000 bats and the other approximately 17,000 bats. We found that Brazilian free-tailed bats emit distinct frequency-modulated (FM_{start}) and constant frequency (CF_{start}) calls during emergence that are significantly different from echolocation calls they emit while foraging. We propose that these calls provide different information for orientation within the emergence column. CF_{start} calls are very similar to social calls used by Brazilian free-tailed bats, suggesting 2 potential functions for this call type. The structure of both the FM_{start} and CF_{start} calls were not related to the number of bats emerging from a roost, although significant structural differences existed between sites. The differences between sites could be associated with the spacing of bats during emergence, because bats appeared to form tighter columns at the larger roost colony compared to the smaller colony. DOI: 10.1644/09-MAMM-A-302.1.

Key words: bats, echolocation, emergence, *Tadarida*

Echolocating bats face a variety of changing behavioral and ecological conditions during flight that may influence the optimal call structure for orientation and prey detection. Correspondingly, most bats exhibit flexibility in echolocation and adjust signal structure to fit the challenges of a specific environment, including the proximity of insect targets (Griffin 1958), amount of vegetative clutter (Kalko and Schnitzler 1993; Obrist 1995; Rydell 1990), size of a flight area (Barclay et al. 1979), and presence of conspecifics (Gillam et al. 2007; Obrist 1995).

The questions of if and how bats alter their echolocation call structure during nightly emergence flights have not been well explored. Individuals exiting a roost in large groups face highly cluttered conditions due to the presence of many other bats in a relatively small air volume. Echolocation may provide an emerging individual with critical information for avoiding collisions with nearby conspecifics but will be hampered by interference and jamming effects from the calls of other bats (Gillam et al. 2007; Ratcliffe et al. 2004;

Ulanovsky et al. 2004). Bats also can face dangers during emergence due to predation risks near the roost (Baker 1962; Lee and Kuo 2001), and echolocation could provide essential details about the position and movements of nearby predators.

Brazilian free-tailed bats (*Tadarida brasiliensis*) are an especially interesting species for investigating echolocation call structure during emergence. In south-central Texas, these bats form large colonies ranging in size from several thousand individuals in building and bridge roosts to millions of bats in large limestone caves (Betke et al. 2008; Cockrum 1969; Davis et al. 1962). Unlike many other species where emergence patterns are diffuse and show little group integrity, bats at larger colonies of *T. brasiliensis* emerge in a tight serpentine column (Wilkins 1989). This column formation is believed to be a tactic for avoiding predation by raptors, which are often present near

roosts during early-evening emergences (Baker 1962; Lee and Kuo 2001; Reichard et al. 2009). Bats emerging in a dense column are separated from each other by very short distances and face the challenge of avoiding collisions with other bats (Betke et al. 2008; Hristov et al. 2008).

The 1st objective of this study was to identify the general call types used by Brazilian free-tailed bats during mass emergence from cave roosts. Simmons et al. (1978) offers the only previous description of the emergence calls of *T. brasiliensis*, having found that bats emerging from a small hole in the side of a building emitted signals that were substantially more broadband than foraging calls. Further, the observed signals generally began with a constant-frequency (CF) component followed by a downward frequency-modulated (FM) sweep. The challenges faced by bats exiting from a small opening, as explored by Simmons et al. (1978), are very different from those experienced when exiting from a large cave colony, and the echolocation signals used under these emergence conditions may differ. We analyzed emergence calls recorded at 2 cave roosts. We also compared emergence calls to foraging calls of *T. brasiliensis* collected from a nearby site.

The 2nd objective of this study was to determine if call structure was correlated with emergence rate, defined as the number of bats emerging per minute. At large roosts of *T. brasiliensis* rates can vary from <100 bats/min to >30,000/min (Fig. 1). We hypothesized that bats adjust their echolocation call structure in response to the emergence rate, similar to how many species actively alter echolocation structure in response to the density of vegetation in an environment. We predicted that during peak emergence periods bats would use shorter, higher-frequency, broader-bandwidth calls compared to periods of sparse emergence. Such signals facilitate highly accurate localization of nearby objects (Schnitzler and Kalko 1998) and should provide critical information for avoiding collisions with other bats in the emergence column. To test this hypothesis we determined if changes in call structure were correlated with the numbers of bats emerging from the roost, as measured from thermal infrared video recordings.

MATERIALS AND METHODS

Methods used in this study were in accordance with policies of the Texas Parks and Wildlife Department, guidelines of the American Society of Mammalogists for the use of wild mammals (Gannon et al. 2007), and the Institutional Animal Care and Use Committees of the University of Tennessee and Boston University.

Field studies.—Audio and thermal infrared video recordings were made at 2 roosts in south-central Texas, Ney Cave (NC), near Bandera, Texas, containing a large maternity colony estimated at 200,000–400,000 bats at the time of the recordings (Betke et al. 2008), and the Selah Chiroptorium (SC) near Johnson City, Texas, a man-made cave that housed several thousand Brazilian free-tailed bats during the period of our study (Betke et al. 2008). Recordings were taken at NC on 26 and 27 June 2006 and at SC on 2 July 2006. We defined the
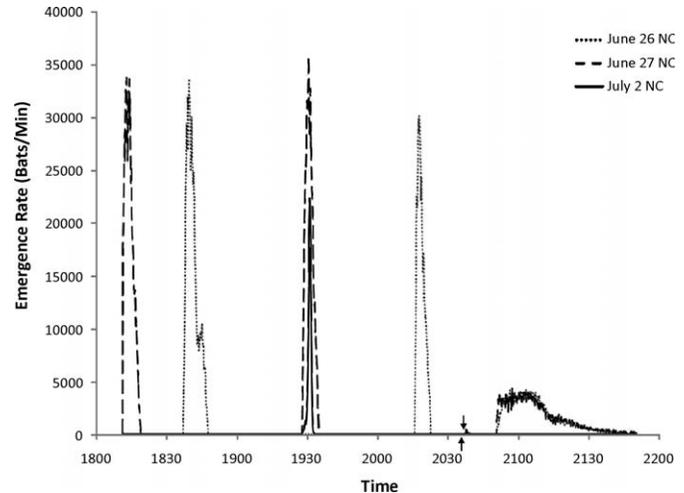

FIG. 1.—Emergence profiles for Ney Cave on 26 June and 27 June 2006 and Selah Chiroptorium on 2 July 2006. Upward-pointing arrow indicates sunset time for 26 June and 27 June 2006 (2036 h) and downward-pointing arrow indicates sunset time for 2 July 2006 (2037 h).

beginning of an emergence as the time when bats began to exit the roost. At SC a clear end to the emergence could be seen when bats stopped exiting the cave. However, it was difficult to determine an exact end point at NC, because bats exited over several hours, and individuals began returning before the last bats had left the cave. Thus, we defined the end of an emergence at NC as the time when a roughly equal number of bats were entering and exiting the cave.

We obtained real-time audio recordings using Avisoft CM16 solid dielectric microphones (frequency response of ±3 dB between 10 and 100 kHz; Avisoft Bioacoustics, Berlin, Germany) mounted on light stands. At each site we selected a height and orientation for each microphone that resulted in the highest-quality recordings. We placed 2 microphones at NC, with 1 oriented perpendicular to the emerging column at a height of 1.5 m and another placed directly below the column at a height of 1 m. Because of the smaller colony size at SC, we used only 1 microphone, which we pointed perpendicular to the emerging column at a height of 1.5 m. At both sites high-speed data acquisition was accomplished with Avisoft's Ultrasound Gate 416 (Avisoft Bioacoustics) connected to a Dell Inspiron laptop (Dell Inc., Round Rock, Texas) running Avisoft RECORDER (Avisoft Bioacoustics). Recordings were 5 min long, but sampling was continuous because no time gap occurred between consecutive recording files. Recordings were made with 16-bit resolution and a 166-kHz sampling rate.

Thermal infrared video was collected in synchrony with audio recordings at both sites. We used a FLIR/Indigo Systems Merlin Mid thermal infrared camera (FLIR/Indigo Systems, Santa Barbara, California) to record bats as they emerged from the roost. The camera acquired 12-bit intensity values in a 320 × 240 digital video format at a rate of 60 frames/s, recorded directly to a computer hard drive (Betke et al. 2008). At NC the optical axis of the camera was oriented perpendicular to the flight path of emerging bats. Because of

the landscape at SC and the bats' direction of flight upon exiting the cave, we were not able to capture all emerging bats from 1 orientation. Thus, we placed the camera at a position that recorded the greatest number of bats. Although this setup meant that we failed to count a small percentage of individuals, video data were used for relative comparisons, thus absolute counts were not critical. Collection of audio and video data was started and stopped simultaneously, allowing for alignment of the 2 data streams during analysis.

Data measurement and analysis.—We identified 2 types of calls produced by emerging bats and conducted separate analyses on each call type. For each study night we selected 1 high-quality call of each type from every 10-s increment of the emergence. To ensure that we did not select multiple calls from the same individual, all calls were separated in our recordings by a minimum of 5 s. Given the large numbers of bats exiting the cave and their rapid emergence flight speed (8.75 m/s ± 1.6 *SD*—N. I. Hristov, pers. obs.), it is highly unlikely that calls emitted >5 s apart are from the same bat.

We obtained acoustic measurements from waveforms (amplitude × time representation) and spectrograms (frequency × time representation) computed using a 1,024-point fast Fourier transform (93.75% overlap—Specht 2010). These settings yielded a spectral resolution of 163 Hz and a temporal resolution of 0.96 ms. For each selected call we measured duration (Dur), maximum frequency (Fmax), minimum frequency (Fmin), and peak frequency (Fpeak; also known as frequency of maximum energy). To determine Dur, the start time (t1) and end time (t2) of each call were measured from the waveform, except during periods of heavy emergence when the high density of calls often did not allow us to take an accurate measurement from the waveform. In such cases we measured Dur directly by determining t1 and t2 from the spectrogram. We tested this method by selecting several calls where the signal waveform could be assessed, measuring Dur from both the waveform and spectrogram, and comparing measurements from the 2 methods. Measurements of Dur were very similar, and when combined with the high temporal resolution of the spectrogram, we are confident that our measurements accurately reflect call duration. Fpeak was defined as the maximum peak in the power spectrum generated for the entire call. Fmax and Fmin were calculated by measuring the maximum peak in the power spectra at t1 and t2 of each call. We chose this method of measuring Fmin and Fmax because of the high density of calls in the data set and issues with obtaining measurements using standard methods (i.e., −15 dB below Fpeak). Bandwidth (BW) was calculated as the difference between Fmax and Fmin of each measured call.

To census Brazilian free-tailed bats, computer vision algorithms were used to automatically count bats. The process was completed in 2 steps, 1st by automatically detecting bats in each video frame and 2nd by tracking each detected bat from frame to frame. Bats successfully detected and tracked for a period of time beyond a set threshold value were tallied automatically to estimate the total number of emerging bats. Data were outputted at 600-frame intervals, which yielded a count of how many bats emerged in a 10-s interval. The sum of all 10-s intervals produced an estimate of the total colony size. Each 10-s count was multiplied by 6 to generate an emergence rate in number of bats per minute. Detailed methods for recording and analyzing thermal video data are explained in Betke et al. (2007, 2008), Hristov et al. (2008), and Kunz et al. (2009).

We aligned our video and audio data so that each 10-s emergence count was associated with measurements of 1 call of each call type from the same 10-s period. Because audio and video recordings were captured synchronously, alignment was easily accomplished. We performed a series of linear regressions to determine if emergence count was associated with each of the 5 call variables for both call types. Because call data were not normally distributed and common transforms did not fix this problem, we conducted nonparametric bootstrap analyses (Sokal and Rohlf 1995). These analyses were conducted in NCSS (Statistical Systems, Kaysville, Utah), using 3,000 bootstrap samples to yield bias-corrected R^2 estimates.

In addition to the 2 call types recorded during emergence, we also obtained measurements from echolocation calls of free-flying *T. brasiliensis* foraging over a nearby cotton field in south-central Texas, which we refer to as foraging calls (Gillam et al. 2007). These calls were recorded and measured using the same equipment described above. We selected 1 call from each of 30 call sequences. Because of nonnormality and unequal sample sizes and variances, we performed 3 nonparametric bootstrap analyses to compare the differences between the 2 emergence call types and the foraging calls. We also used bootstrap comparisons to assess effects of location and date on call structure. Each analysis involved resampling the data set 3,000 times and computing a bootstrap *P*-value and 95% confidence interval. Bootstrap comparisons were performed in SPSS 15.0 (SPSS Inc., Chicago, Illinois) using the BOOTDIFF macro (Hayes 2005).

RESULTS

On 26 June the emergence at NC began at 1837 h and ended at 2144 h CDT. During these 3+ h we observed 3 distinct periods of emergence separated by intervals of no activity (11-min emergence, 88-min break, 6-min emergence, 26-min break, and 56-min emergence; Fig. 1). Similarly, on 27 June bats began exiting the cave at 1811 h and stopped at 2143 h, with 3 separate emergences (9-min emergence, 69-min break, 8-min emergence, 66-min break, and 60-min emergence; Fig. 1). The substantially shorter emergence at SC on 2 July started at 1928 h and stopped at 2042 h, with 2 distinct periods of activity (6-min emergence, 63-min break, and 5-min emergence; Fig. 1). Total colony size estimates for NC were 196,210 bats on 26 June and 215,410 bats on 27 June. Emergence rates on these 2 nights varied from 6 to 35,688 bats/min. The final count at SC was 16,210 bats, with a range of emergence rates from 6 to 22,284 bats/min.

Recordings typically contained a large number of calls. We found that bats most commonly emit 2 major types of calls

during emergence. Both call types regularly included multiple harmonics, although we focused our analysis solely on the fundamental signal. The 1st call type begins with a broadband, downward FM sweep, followed by a short quasi-CF (QCF) region (Fig. 2a). A short downward FM sweep is sometimes (<50%) found at the end of the call. We refer to this signal type as an FM_{start} call. We measured a total of 944 FM_{start} calls, 434 from NC on 26 June, 451 from NC on 27 June, and 59 from SC on 2 July. The 2nd call type recorded during emergence begins with a short CF component followed by a broadband, downward FM sweep (Fig. 2b). In some cases an initial upward FM sweep was present, giving the appearance of a hook at the beginning of the call (Fig. 2c). We refer to this signal type as a CF_{start} call. We measured a total of 861 CF_{start} calls, 422 from NC on 26 June, 402 from NC on 27 June, and 37 from SC on 2 July. On rare occasions we encountered calls that appeared to be intermediate in structure between FM_{start} and CF_{start} calls. We did not identify these signals as a 3rd call type because they were very uncommon.

The 2 documented call types were significantly different from each other ($P < 0.0001$ for all call variables; Table 1). On average, CF_{start} calls were shorter, lower in frequency (Fmin, Fmax), and narrower in BW compared to FM_{start} calls. However, Fpeak was significantly higher for CF_{start} calls. In general, Fpeak of FM_{start} calls was located in the terminal QCF section of the signal, and Fpeak of CF_{start} calls was most often within the initial, high-frequency CF section of the call. Both FM_{start} and CF_{start} calls (Figs. 2a–c) were substantially shorter, broader in BW, and higher in frequency than calls recorded from solitary, free-flying bats foraging over a large cotton field ($P < 0.0001$ for all variables).

We found a significant effect of location. FM_{start} calls from NC were shorter, higher frequency, and wider in BW than calls from SC ($P < 0.0001$ for all call variables). CF_{start} calls from NC had a shorter Dur ($P = 0.02$) and lower Fpeak ($P = 0.006$), although Fmin, Fmax, and BW did not differ significantly between locations. The largest difference in average call structure between sites was the 14- kHz-higher Fpeak of CF_{start} calls at NC compared to SC (Table 1).

We did not find a meaningful relationship between call structure and emergence rate (Figs. 3 and 4). Analysis of FM_{start} calls revealed that emergence rate explained little variation in any of the call variables at both caves. R^2 values were for NC: Dur = 0.09, Fmin = 0.09, Fmax = 0.002, Fpeak = 0.13, BW = 0.01; and for SC: Dur = 0.1, Fmin = 0.16, Fmax = 0.06, Fpeak = 0.02, BW = 0.02. The same pattern of low R^2 values was observed for the relationship between emergence rate and CF_{start} call parameters. They were for NC: Dur = 0.08, Fmin = 0.08, Fmax = −0.014, Fpeak = −0.05, BW = 0.007; and for SC: Dur = 0.1, Fmin = 0.16, Fmax = 0.06, Fpeak = 0.02, BW = 0.02.

DISCUSSION

Brazilian free-tailed bats emerging from roosts in dense columns face a major sensory processing problem, dubbed by
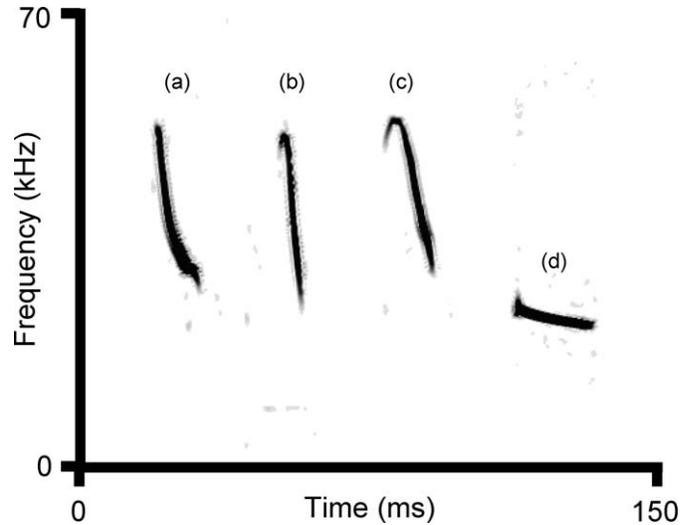

Fig. 2.—Spectrogram depicting an assemblage of recorded call types. a) Frequency-modulated (FM_{start}) call recorded during 26 June emergence at Ney Cave. b) Constant-frequency (CF_{start}) call with a short CF section, recorded during 26 June emergence at Ney Cave. c) CF_{start} call with an initial upward FM sweep, recorded during 2 July 2006 emergence from Selah Chiroptorium. d) Echolocation call recorded from *Tadarida brasiliensis* foraging over a cotton field in south-central Texas in May 2005.

Ulanovsky and Moss (2008) as the ''cocktail party nightmare.'' During emergence each individual is faced with identifying the returning echoes of their own calls amongst the multitude of calls and echoes of nearby conspecifics. Further, the high density of bats in the near environment will result in the production of many echoes for every emitted call. These conditions lead to forward masking, in which echoes return before the bat has finished pulse emission (Jones and Holderied 2007), and backward masking, in which echoes overlap with each other (Jones and Holderied 2007; Kalko and Schnitzler 1993). Overall, an individual bat can perceive tens to hundreds of thousands of echoes during an emergence (Ulanovsky and Moss 2008). Determining the structure of emergence calls should help us understand how bats cope with such a noisy signaling environment and effectively orient within the column.

Compared to the calls used when foraging in open areas (Gillam et al. 2007; Ratcliffe et al. 2004), the short, high-frequency, broadband signals that *T. brasiliensis* uses when emerging from caves provide more accurate estimates of target position and a shorter maximum detection distance (Schnitzler and Kalko 2001), both of which are important features for avoiding collisions in a highly cluttered habitat. Further, the distance at which ranging error is minimized and target localization estimates are most accurate, known as the ''distance of focus'' (Holderied et al. 2006), will be substantially closer to the bat, further increasing the accuracy of information about objects in the near environment. Similar adjustments to signal structure are seen in many bat species flying in complex, cluttered habitats, such as the interior of a forest (Kalko and Schnitzler 1993; Obrist 1995; Rydell 1990). Our results suggest that bats perceive emergence in a tight
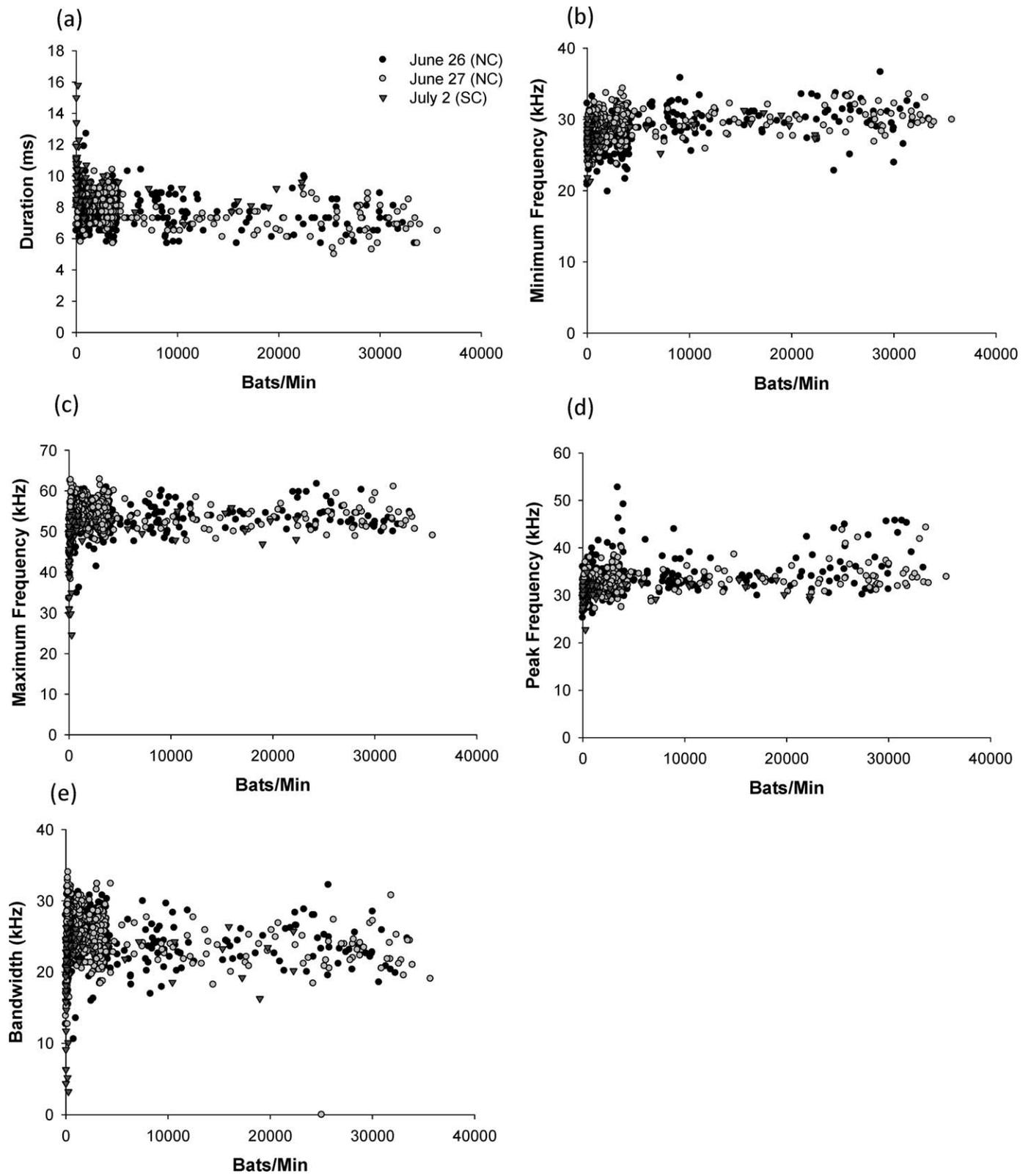
FIG. 3.—Scatter plots of each frequency-modulated (FM$_{start}$) call variable against emergence rate (bats/min): a) Dur, b) Fmin, c) Fmax, d) Fpeak, and e) BW. See ''Materials and Methods'' for explanation of call variables.

TABLE 1.—Mean (*SD*) of the 5 measured call variables. Data are partitioned by call type (frequency-modulated [FM_{start}], constant-frequency [CF_{start}], and foraging calls) and location (Ney Cave [NC] and Selah Chiroptorium [SC]). See ''Materials and Methods'' for explanation of call variables.

	FM_{start}		CF_{start}		
	NC	SC	NC	SC	Foraging
n	885	59	824	37	30
Dur (ms)	7.9 (1.0)	9.8 (1.6)	6.0 (0.9)	7.5 (1.8)	12.8 (1.1)
Fmin (kHZ)	28.8 (2.1)	27.5 (2.0)	27.1 (3.4)	26.6 (2.9)	22.7 (1.5)
Fmax (kHZ)	53.6 (3.5)	47.8 (7.0)	49.5 (3.1)	48.2 (3.9)	27.0 (3.0)
Fpeak (kHZ	32.9 (2.8)	30.8 (1.7)	46.8 (6.5)	32.9 (3.7)	24.5 (1.6)
BW	24.8 (3.2)	20.3 (5.8)	22.4 (3.9)	21.6 (4.6)	4.3 (2.4)

column as a highly cluttered habitat and adjust their echolocation call structure to maximize echo reception and minimize the chance of collisions.

We found that bats emerging from dense cave colonies commonly produced 2 types of calls. FM_{start} calls resembled those emitted by *T. brasiliensis* flying in a small room (Bohn et al. 2008; Simmons et al. 1978) and calls used in late approach phase of echolocation as a bat nears an insect target (Schwartz et al 2007). The downward FM sweep sometimes found at the end of these calls has been seen in a variety of other bat species (Barclay et al. 1979; Fenton and Bell 1981; Schnitzler and Kalko 2001). Although different from their foraging calls, FM_{start} calls appear to be commonly used by this species when detailed information about nearby targets is needed. CF_{start} calls are similar to those described by Simmons et al (1978) from *T. brasiliensis* emerging from a small hole in a building, and resemble the CF-FM echolocation calls reported for bats in the family Mormoopidae (Ibáñez et al. 1999; O'Farrell and Miller 1997). It is important to note that even though our large sample size means that minute differences are likely to be detected as statistically significant, our observations that absolute differences between call types (in temporal and spectral features) are large indicate that the observed discrepancies are also biologically significant. This is especially apparent with Fpeak, which differed by an astounding 14 kHz between FM_{start} and CF_{start} calls.

It is not clear why bats emit 2 different types of calls during emergence. One explanation is that each call type provides different information to an emerging bat. Bats in flight move their head from side to side, which changes the direction of sound emission between calls (Simmons 1973). It is likely that bats near the edge of the emergence column, which are the individuals most likely to be recorded, direct some calls toward the highly cluttered center of the column, whereas other calls are oriented toward the uncluttered environment outside of the emergence column. We propose that individuals of *T. brasiliensis* emit CF_{start} calls when directing signals toward the column interior and use echo information to regulate their spatial position in reference to the locations of nearby conspecifics. The transition from CF to FM call components provides a precise alignment point for cross correlation in the brain and should facilitate accurate assessment of target range (Bradbury and Vehrencamp 1998). Further, the concentration of power (i.e., Fpeak) in the high-frequency CF section will shorten the maximum detection distance, an optimal feature if bats are most interested in the details of their immediate surroundings. Alternatively, we propose that FM_{start} calls are emitted when bats direct signals outside of the column. Although a short duration and broad BW means that FM_{start} calls also provide accurate range estimates, the presence of the low-frequency, high-amplitude QCF region at the end of the call would lead to longer detection distances that may be useful for assessing the presence of predators or other objects to be avoided. Although it seems plausible that a mix of the 2 call types can provide the information needed for efficient navigation within the emergence column and assessment of hazards beyond the column, detailed descriptions of column structure and flight patterns are needed to test this hypothesis.

The CF_{start} calls are essentially identical to 2 types of social calls emitted by Brazilian free-tailed bats. Bohn et al (2008) reported that captive Brazilian free-tailed bats emitted ''food solicitation'' calls prior to being fed by a handler, and Schwartz et al. (2007) documented the use of CF-FM communication buzzes by captive bats during aggressive interactions associated with feeding, such as when bats chased other individuals away from a feeding dish. Although we could not assess the function of CF_{start} calls in *T. brasiliensis*, the aforementioned studies of captive bats clearly indicate similar signals have a role in social communication. Hence, it is possible that the CF_{start} call emitted during emergence is not used to gather information about the surrounding environment but rather serves an unknown social function. Alternatively, the described social calls produced by bats in laboratory colonies could be an artifact of captivity. If CF_{start} calls are produced in wild populations during emergence, an event immediately prior to foraging, it is plausible that captive bats could emit similar sounds in anticipation of feeding. Further documentation of social call function in wild populations of *T. brasiliensis* is needed to examine these possibilities.

Our finding that neither FM_{start} nor CF_{start} calls change in reference to the numbers of individuals exiting the roost does not support our hypothesis that bats actively adjust their echolocation in response to the intensity of the emergence. One possible explanation for this result is that emergence rate changes over time, but the density of bats stays the same (i.e., the higher the emergence rate, the wider the column expands so that bats remain at a constant distance from each other). Both visual observations by the authors and preliminary data from 3-dimensional reconstructions of the emergence column (N. I. Hristov, pers. obs.) strongly indicate that this is not the case, and that density of the column is directly proportional to emergence rate.

We found that the structure of both FM_{start} and CF_{start} calls differed between caves. Differences may be related to the much greater population size of *T. brasiliensis* at NC compared to SC; average emergence rate was 4,897 bats/min at NC and 3,490 bats/min at SC. Although we did not quantify
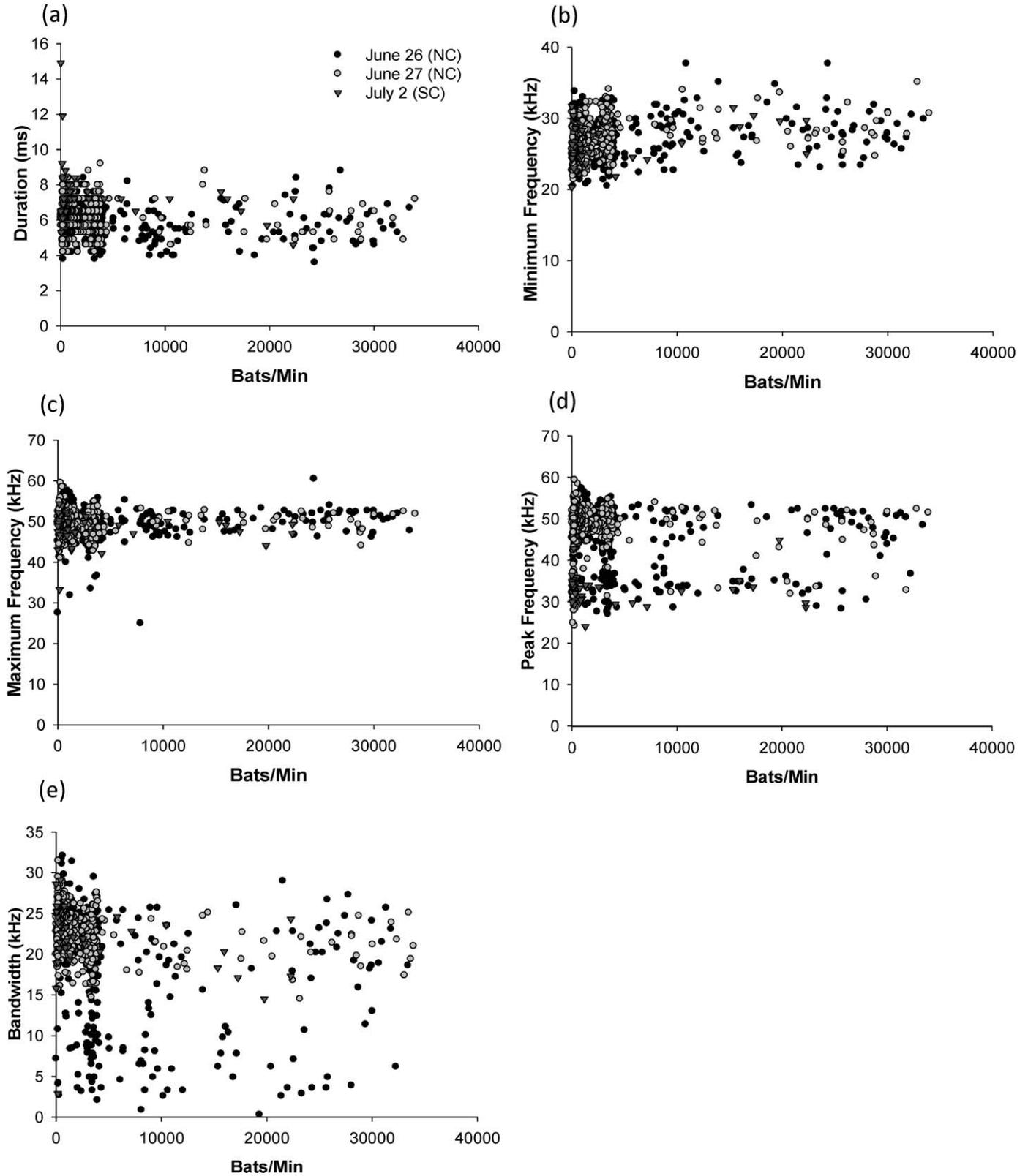
FIG. 4.—Scatter plots of each constant frequency (CF$_{start}$) call variable against emergence rate (bats/min): a) Dur, b) Fmin, c) Fmax, d) Fpeak, and e) BW. See ''Materials and Methods'' for explanation of call variables.

the size and density of the emerging column, visual assessments indicate that bats are spaced closer together at NC than at SC. Similar to the comparison of emergence and foraging signals, calls at NC will travel shorter distances and provide more accurate target range estimates. The reason for the large difference in Fpeak between sites is not obvious, although it could be related to density differences. Higher-frequency signals are more attenuated and travel shorter distances, which decreases the interference produced by conspecific calls and should allow bats to be spaced closer together. Thus, the use of calls with higher Fpeak at a very large roost could serve as a form of collective jamming avoidance. Future testing is necessary to determine if Fpeak of calls recorded at different caves is associated with colony size.

The high signal-to-noise ratio faced during echo processing is a major issue for bats echolocating during a mass emergence. Laboratory studies with *Eptesicus fuscus* have shown that the accuracy of target ranging decreases substantially in the presence of noise signals that resemble a bat's original call (Masters and Raver 1996). Previous studies of jamming avoidance in molossids suggest that bats have limited sensory-processing capabilities in the presence of even 1 conspecific (Gillam et al. 2007; Ulanovsky et al. 2004), begging the questions: Are emerging bats deriving any useful sensory information from echolocation, and if not, why do they continue to echolocate? Investigations of the signal-to-noise ratios experienced by emerging bats and the effect of this interference on echo reception will provide further insight into the signal processing abilities of Brazilian free-tailed bats and the general functions of bat echolocation.

LITERATURE CITED

BAKER, J. 1962. The manner and efficiency of raptor depredations on bats. Condor 64:500–503.

BARCLAY, R. M. R., M. B. FENTON, AND D. W. THOMAS. 1979. Social behavior of the little brown bat, *Myotis lucifugus*. 2. Vocal communication. Behavioral Ecology and Sociobiology 6:137–146.

BETKE, M., D. E. HIRSH, A. BAGCHI, N. I. HRISTOV, N. C. MAKRIS, AND T. H. KUNZ. 2007. Tracking large variable numbers of objects in clutter. Pp. 1–8 in Proceedings of the IEEE Computer Science Society Conference on Computer Vision and Pattern Recognition, Minneapolis, Minnesota, June 2007.

BETKE, M., ET AL. 2008. Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. Journal of Mammalogy 89:18–24.

BOHN, K. M., B. SCHMIDT-FRENCH, S. T. MA, AND G. D. POLLAK. 2008. Syllable acoustics, temporal patterns, and call composition vary with behavioral context in Mexican free-tailed bats. Journal of the Acoustical Society of America 124:1838–1848.

BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Principles of animal communication. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

COCKRUM, E. L. 1969. Migration in the guano bat, *Tadarida brasiliensis*. Miscellaneous Publications, Museum of Natural History, University of Kansas 51:303–336.

DAVIS, R. B., C. F. HERREID, AND H. L. SHORT. 1962. Mexican free-tailed bats in Texas. Ecological Monographs 32:311–346.

FENTON, M. B., AND G. P. BELL. 1981. Recognition of species of insectivorous bats by their echolocation calls. Journal of Mammalogy 62:233–243.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

GILLAM, E., N. ULANOVSKY, AND G. F. MCCRACKEN. 2007. Rapid jamming avoidance in biosonar. Proceedings of the Royal Society of London, B. Biological Sciences 274:651–660.

GRIFFIN, D. R. 1958. Listening in the dark. Yale University Press, New Haven, Connecticut.

HAYES, A. F. 2005. Statistical methods for communication science. Lawrence Erlbaum Associates, Mahwah, New Jersey.

HOLDERIED, M. W., G. JONES, AND O. VON HELVERSEN. 2006. Flight and echolocation behaviour of whiskered bats commuting along a hedgerow: range-dependent sonar signal design, Doppler tolerance and evidence for 'acoustic focusing.' Journal of Experimental Biology 209:1816–1826.

HRISTOV, N. I., M. BETKE, AND T. H. KUNZ. 2008. Applications of thermal infrared imaging for research in aeroecology. Integrative and Comparative Biology 48:50–59.

IBÁÑEZ, C., A. GUILLÉN, J. JUSTE B., AND J. L. PÉREZ-JORDÁ. 1999. Echolocation calls of *Pteronotus davyi* (Chiroptera: Mormoopidae) from Panama. Journal of Mammalogy 80:924–928.

JONES, G., AND M. W. HOLDERIED. 2007. Bat echolocation calls: adaptation and convergent evolution. Proceedings of the Royal Society of London, B. Biological Sciences 274:905–912.

KALKO, E. K. V., AND H. U. SCHNITZLER. 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight—implications for habitat use and prey detection. Behavioral Ecology and Sociobiology 33:415–428.

KUNZ, T. H., M. BETKE, N. I. HRISTOV, AND M. VONHOF. 2009. Methods for assessing colony size, population size, and relative abundance of bats. Pp. 133–157 in Ecological and behavioral methods for the study of bats (T. H. Kunz and S. Parsons, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

LEE, Y. F., AND Y. M. KUO. 2001. Predation on Mexican free-tailed bats by peregrine falcons and red-tailed hawks. Journal of Raptor Research 35:115–123.

MASTERS, W. M., AND K. A. S. RAVER. 1996. The degradation of distance discrimination in big brown bats (*Eptesicus fuscus*) caused by different interference signals. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 179:703–713.

OBRIST, M. K. 1995. Flexible bat echolocation—the influence of individual, habitat and conspecifics on sonar signal-design. Behavioral Ecology and Sociobiology 36:207–219.

O'FARRELL, M. J., AND B. W. MILLER. 1997. A new examination of echolocation calls of some neotropical bats (Emballonuridae and Mormoopidae). Journal of Mammalogy 78:954–963.

RATCLIFFE, J., ET AL. 2004. Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*. Canadian Journal of Zoology 82:966–971.

REICHARD, J. D., L. E. GONZALEZ, C. M. CASY, L. C. ALLEN, N. I. HRISTOV, AND T. H. KUNZ. 2009. Evening emergence behavior and seasonal dynamics in large colonies of Brazilian free-tailed bats. Journal of Mammalogy 90:1478–1486.

RYDELL, J. 1990. Behavioral variation in echolocation pulses of the northern bat, *Eptesicus nilssoni*. Ethology 85:103–113.

SCHNITZLER, H. U., AND E. K. V. KALKO. 1998. How echolocating bats search and find food. Pp. 183–196 in Bat biology and conservation (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

SCHNITZLER, H. U., AND E. K. V. KALKO. 2001. Echolocation by insect-eating bats. BioScience 51:557–569.

SCHWARTZ, C., J. TRESSLER, H. KELLER, M. VANZANT, S. EZELL, AND M. SMOTHERMAN. 2007. The tiny difference between foraging and communication buzzes uttered by the Mexican free-tailed bat, *Tadarida brasiliensis*. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 193:853–863.

SIMMONS, J. A. 1973. The resolution of target range by echolocating bats. Journal of the Acoustical Society of America 54:157–173.

SIMMONS, J. A., ET AL. 1978. Echolocation by free-tailed bats (*Tadarida*). Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 125:291–299.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W. H. Freeman and Company, New York.

SPECHT, R. 2010. Avisoft SasLab Pro user's guide for version 5.0. Avisoft Bioacoustics, Berlin, Germany. http://www.avisoft.com/SASLabPro.pdf. Accessed 30 March 2010.

ULANOVSKY, N., M. B. FENTON, A. TSOAR, AND C. KORINE. 2004. Dynamics of jamming avoidance in echolocating bats. Proceedings of the Royal Society of London, B. Biological Sciences 271:1467–1475.

ULANOVSKY, N., AND C. F. MOSS. 2008. What the bat's voice tells the bat's brain. Proceedings of the National Academy of Sciences 105:8491–8498.

WILKINS, K. T. 1989. *Tadarida brasiliensis*. Mammalian Species 331:1–10.