

Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*

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Abstract: The Brazilian free-tailed bat, *Tadarida brasiliensis* (Saint-Hilaire, 1824), uses calls that represent a broad continuum of design variation which is dependent upon habitat and situation, and exhibits characteristic changes in call design as bats close in on airborne targets. Here we demonstrate the influence of conspecifics on call design. We found that the peak frequency used in calls varies more as the number of bats flying in the same space increases (measured from single bats and pairs of bats). We investigated this phenomenon through comparing call-parameter differences found between two bats recorded flying together (actual pairs) with call-parameter differences between two bats each recorded flying alone at different locations that were randomly assigned to one another (virtual pairs). We found that actual pairs of bats used calls which differed in peak frequency more so than did virtual pairs. This result is particularly striking given that these frequency differences were greater between bats in the same space than between bats in two different habitats. We argue that these differences indicate that this species is practicing jamming avoidance, air traffic control, or both.

Résumé : Le tadaride du Brésil, *Tadarida brasiliensis* (Saint-Hilaire, 1824), émet des appels qui présentent une gamme étendue de variations de structure en fonction de l'habitat et de la situation et il change de façon caractéristique la structure de son appel au moment où les chauves-souris attaquent des cibles aériennes. Nous démontrons l'influence des chauves-souris de la même espèce sur la structure de l'appel. La fréquence maximale utilisée dans les appels varie plus lorsque le nombre de chauves-souris qui volent dans un même espace augmente (d'après des enregistrements de chauve-souris solitaires et de paires de chauves-souris). Nous avons étudié ce phénomène en comparant les différences dans les caractéristiques des appels enregistrés chez des paires de chauves-souris qui volent ensemble (paires réelles) avec les différences enregistrées entre deux chauves-souris qui volent seules en deux endroits différentes et qui sont associées l'un à l'autre de façon aléatoire (paires virtuelles). Les appels des paires réelles diffèrent par leur fréquence maximale plus que ceux des paires virtuelles. Cette observation est d'autant plus remarquable que ces différences de fréquence sont plus grandes entre des chauves-souris qui volent dans le même espace qu'entre des chauves-souris qui occupent des habitats différents. Nous croyons que ces différences indiquent que cette espèce évite le brouillage des signaux ou effectue un contrôle du trafic aérien ou alors fait les deux opérations à la fois.

[Traduit par la Rédaction]

Introduction

Microchiropteran bats vary the design features of their echolocation calls according to task. Changes across feeding sequences are best known (Griffin et al. 1960; Kick and Simmons 1984; Surlykke and Moss 2000; Ratcliffe and Dawson 2003), whether the target is a flying insect (Griffin et al. 1960; Kalko and Schnitzler 1989), a perched moth (Ratcliffe and Dawson 2003), or a swimming fish (Suthers

1965). These changes can be considerable across the attack sequence and involve intensity, as well as frequency- and time-dependent parameters (e.g., Schumm et al. 1991). Changes in call parameters may also reflect factors such as the hearing ability of potential prey (e.g., Fullard et al. 2003), level of clutter (echoes from other than the object of interest; see Kalko and Schnitzler 1993; Obrist 1995), or presence of conspecifics (Suthers 1965). The influence of conspecifics on call design has been proposed to reflect a

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jamming avoidance response (i.e., individuals alter the features of their emissions in the presence of conspecifics to minimize interference), active communication (i.e., air traffic control), or both (Habersetzer 1981; Fenton 1985; Jones et al. 1994; Obrist 1995; Ulanovsky et al. 2004).

Two or more animals using active orientation in the same space might necessitate jamming avoidance to prevent the returning signals of one individual from being confused with those emitted by another (Dusenbery 1992). The situation is best documented for electric fish where both wave- and pulse-emitting species use different rules to avoid conspecific jamming (Heiligenberg 1977, 1991; Kawasaki 1997; Metzner 1999). The situation is less clear for echolocating bats (see Habersetzer 1981; Jones et al. 1994; Obrist 1995). Lesser mouse-tailed bats (*Rhinopoma hardwickei* Gray, 1831) change the frequencies dominating their calls when flying in the presence of conspecifics (Habersetzer 1981), and some vespertilionids also may change call features in the same situation (Obrist 1995; Surlykke and Moss 2000). Although referred to as jamming avoidance (e.g., Habersetzer 1981; Obrist 1995; Surlykke and Moss 2000), support for this interpretation is not as strong as that for the jamming avoidance response in electric fish: described variation may result from there simply being greater numbers of bats (and, therefore, a wider variety of individual call designs) in group samples (e.g., Masters et al. 1995). However, laboratory attempts to jam echolocation have met with some success (Jones et al. 1994; Masters and Raver 1996), indicating that jamming avoidance, if practiced, would benefit wild bats foraging in numbers.

Published data about echolocation calls of the Brazilian free-tailed bat, *Tadarida brasiliensis* (Saint-Hilaire, 1824), report an extremely wide range of frequencies in their calls as a result of different environments and activities (e.g., Simmons et al. 1978; Fenton and Bell 1981), providing some of the first evidence that bats use a wide variety of echolocation call designs (Simmons et al. 1979). *Tadarida brasiliensis* is a widespread New World species with both resident and migratory populations (Wilkins 1989). At times, these bats form huge colonies (millions of individuals) in natural (caves) and artificial (bridges, buildings) roosts in both rural and urban settings (Wilkins 1989), and forage both singly and in groups. Because many *T. brasiliensis* often share roosts, foraging areas, and fly in high densities, these bats may vary echolocation calls either for jamming avoidance or as a means of communication. Although the potential effects of inter-individual signal interference (i.e., jamming) have dominated our interpretation of the supposedly interactive call variation observed in groups of bats, changes in echolocation call design could also be used to highlight individual identities and allow bats to keep track of others sharing the same space (i.e., air traffic control). The two possibilities are not mutually exclusive.

While visually inspecting calls for another study on the use of urban space (Avila-Flores 2003), we noticed that there appeared to be more variation in call frequencies when bats flew with conspecifics than alone. We tested the prediction that the increased variability is due to bats changing their echolocation calls in the presence of others, instead of simply the result of a greater number of bats in the sample, by comparing actual and "virtual" pairs of bats.

Methods

Study sites

We recorded the echolocation calls of *T. brasiliensis* at three locations in Mexico City. The recordings were made between late May and late August 2002 at Parque San Juan de Aragón, Monumento a la Revolución, and Plaza Cuicuilco. The first site was the shore of an open, artificial lake within a large urban park, whereas the other locations corresponded to open squares within urban areas illuminated by streetlights. All sites fell within 6 km of the central square of the city (19°43'25"N, 99°13'52"W), and each was at least 2 km from the nearest one.

Acoustic recording

Recordings were made at each location between the hours of 2030 and 0200 on clear nights. We recorded 204 sequences, each 60 s in duration, using the high-frequency analog output of the bat detector (Model D980; Pettersson Elektronik AB, Uppsala, Sweden) connected to a Dell Latitude portable computer running BatSound Pro version 3.30 (Pettersson Elektronik AB licensed to M.B. Fenton). Connection to the computer was made through a high-speed sound card (DAQCard-6062E; National Instruments, Austin, Texas, USA), and incoming signals were filtered at the input using a F2000 control filter (Pettersson Elektronik AB) set at low gain. Recording settings were defined both in the software (frequency sampling = 250 kHz, gain = 2, 12 bits/sample) and in the bat detector (dial set to 10% gain). The bat detector was positioned at 45° to the horizontal 1.2 m above ground.

Call-sequence selection

We selected a total of 30 sequences from three locations consisting of 10 consecutive search-phase echolocation calls, selecting sequences with the greatest signal to noise ratios. We chose sequences in which no two calls exhibited temporal overlap. We assigned each recorded sequence to one of two situations: solitary bats (15 sequences, 5 per location) and two bats flying in close proximity (15 sequences, 5 per location). By visually, and sometimes acoustically, examining the recordings in BatSound Pro, we could always identify situations where we had recorded the calls of one bat as evidenced by regularly repeated echolocation calls with a regular interpulse interval (Fig. 1b), reflecting the association between wingbeat and call production (Speakman and Racey 1991). We used variations in interpulse intervals to identify call sequences involving two bats, whereas a combination of timing, amplitude, and frequency features allowed us to recognize which of the calls corresponded to one bat or the other. In searching for useable sequences in BatSound Pro, we used a Butterworth filter (filter order 2) to remove ambient noise below 20 kHz after ensuring that this setting would not remove any call features.

Call analysis

We analyzed calls by first examining *.wav files in BatSound Pro and then transferring this digital information to Matlab version 6.5 (The MathWorks Inc., Natick, Massachusetts, USA; licensed to M.B. Fenton). Specifically, we marked the beginning of each sequence and the beginning

Table 1. Median values (and interquartile ranges) for three call parameters from search-phase calls of single Brazilian free-tailed bats, *Tadarida brasiliensis*, flying alone in three locations.

Location	Parameter		
	Duration (ms)	Peak frequency (kHz)	Bandwidth (kHz)
Plaza Cuicuilco	14.2 (13.8–16.0)	24.8 (23.9–25.2)	2.73 (1.68–3.13)
Monumento a la Revolución	12.3 (12.1–14.5)	24.1 (22.8–25.4)	5.0 (3.06–5.59)
Parque San Juan de Aragón	13.6 (13.2–15.0)	25.0 (24.9–26.8)	2.49 (1.52–2.92)

and end of each echolocation call in BatSound Pro, assessing these features using spectrograms and oscillograms, respectively. We saved the time markers as a tab-delineated *.txt file and the BatSound Pro *.wav file as a standard *.wav file, and imported both into a custom program in Matlab. The output of the Matlab analysis provided duration of calls (ms), interpulse intervals (ms), peak frequencies (kHz), and high and low frequencies (kHz). Peak frequency was taken directly from power spectra (1024 point fast Fourier transform (FFT)), as were high and low frequencies (–10 dB from peak on right and left sides, respectively). Bandwidth was calculated by subtracting the low frequency from the high frequency.

Statistical analysis

We used SigmaStat version 3.0 (SPSS Inc., Chicago, Illinois, USA) to test for habitat-induced variation in echolocation calls by comparing three call parameters (duration, peak frequency, and bandwidth) among the three locations. We took measurements from five sequences of 10 search-phase calls of single bats flying alone per location and entered the mean for each sequence for each parameter into three Kruskal–Wallis tests (one for each parameter) (Zar 1996). We examined the influence of social setting on call parameters by testing for homogeneity of variance for call parameters between single bats and bats flying in pairs.

Actual versus virtual pairs of bats: creation of virtual pairs

To compare echolocation calls between bats flying alone and in the presence of another bat, we compared actual pairs of bats with virtual pairs for the same three parameters given above. Bats recorded flying alone at two different locations were randomly matched for the creation of these virtual pairs. Each sequence from the pool of single individual call sequences once used was not replaced. We matched sequences from different locations to minimize pseudo-replication (Hurlbert 1984). There are thousands of bats in the local population (Sánchez et al. 1989) which in itself suggests that resampling the same individual at two different locations would be extremely unlikely. For actual pairs of bats recorded at the three locations, the absolute values of the difference between the mean values of calls from bat one and the mean values of calls for bat two ($n = 4$ to 6 calls/bat) were used as data. For virtual pairs, the absolute values of the difference between the mean values of five calls from each of two single bats flying alone were used as data. These data were analyzed using Mann–Whitney U tests.

Results

In sequences recorded from single bats, none of the three

call parameters tested differed significantly between locations (Kruskal–Wallis test: duration, $H_2 = 2.665$, $p = 0.264$; peak frequency, $H_2 = 3.020$, $p = 0.221$; bandwidth, $H_2 = 4.460$, $p = 0.108$) (Table 1). Solitary *T. brasiliensis* consistently produced shallow frequency-modulated search-phase echolocation calls lasting, on average, 13.95 ± 0.37 ms (range 11.6–16.5 ms), with bandwidths averaging 3.04 ± 0.38 kHz (range 0.99–5.82) (Fig. 1a). The mean frequencies of the calls were variable, with peak frequency from 22.64 to 28.00 kHz (24.88 ± 0.35 kHz), highest frequency from 24.34 to 29.78 kHz (27.01 ± 0.41 kHz), and lowest frequency from 20.85 to 26.75 kHz (23.97 ± 0.41 kHz).

To compare variability in call parameters when bats were flying alone or in pairs, we calculated the means for 5 calls of single bat sequences ($n = 14$) and 5 calls of one bat flying in a pair ($n = 14$), and tested for homogeneity of variance between the two samples with equal numbers of bats. Variances were not homogenous for peak frequency (Levene statistic, $p = 0.49$) or for duration ($p = 0.46$), but were homogenous for bandwidth ($p = 0.337$). Means and SEs reflected this increased variability in call parameters for bats flying together compared with the variability in solitary bats (duration, solitary bat vs. one bat in pair = 13.83 ± 0.36 vs. 13.36 ± 0.83 ms; peak frequency, solitary bat vs. one bat in pair = 25.17 ± 0.33 vs. 25.67 ± 0.68 ms; bandwidth, solitary bat vs. one bat in pair = 2.85 ± 0.38 vs. 2.80 ± 0.45 kHz).

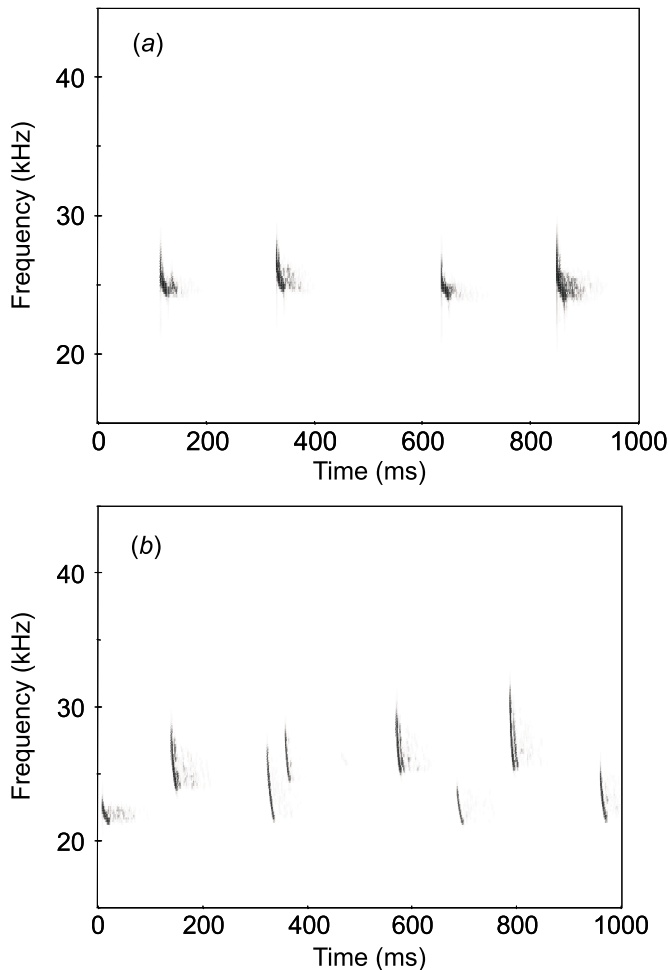
Because we did not find significant differences in call parameters among locations, we used call sequences from two individuals at different locations to create the virtual pairs of bats. All actual pairs of bats were recorded at these locations. There were no significant differences between actual and virtual pairs of bats for the absolute values of the difference in call duration (Mann–Whitney U test, $U = 19.5$, $p = 0.535$) and bandwidth ($U = 11.0$, $p = 0.097$). However, differences in peak frequency ($U = 2.0$, $p = 0.004$) were greater for actual pairs than virtual pairs (Table 2). This suggests that individuals flying in the same space adjust their peak frequency so that the between-individual differences are greater within actual pairs flying in the same space than between two bats flying alone at different locations.

When more than one *T. brasiliensis* flew in the same airspace, we sometimes recorded non-echolocation calls that we interpreted as social calls (Figs. 2a and 2b). Compared with echolocation calls, social calls were more complex and variable. One of the most common social calls consisted of rapid emission of bouts of two or more steep, short calls (Fig. 2a), but sometimes we recorded successions of steep, short calls at irregular frequencies and intervals (Fig. 2b). Less commonly recorded were social calls oscillating in frequency producing V- and W-shaped spectrogram displays (Fig. 2b). The irregular emissions and undulating frequency modulation (i.e., downward sweeping portions followed by

Table 2. Median values (and interquartile ranges) of the absolute differences in values between one *T. brasiliensis* and a second *T. brasiliensis* of actual and virtual pairs for three call parameters ($n = 7$ pairs per group).

	Duration (ms)	Peak frequency (kHz)	Bandwidth (kHz)
Actual pairs	1.8 (1.18–2.97)	2.5 (2.06–3.1)	0.84 (0.45–1.23)
Virtual pairs	1.39 (0.91–2.59)	0.6 (0.43–1.07)	1.72 (1.25–2.91)

Fig. 1. Spectrograms (1024 point fast Fourier transform (FFT)) illustrating a single Brazilian free-tailed bat, *Tadarida brasiliensis*, flying in the same habitat (a) as two *T. brasiliensis* flying in the same airspace at roughly the same direction and distance from the microphone (b).



upward sweeping portions) of these calls should render them less suitable for orientation and insect capture than the downward sweeping, frequency-modulated calls typically associated with echolocation.

Discussion

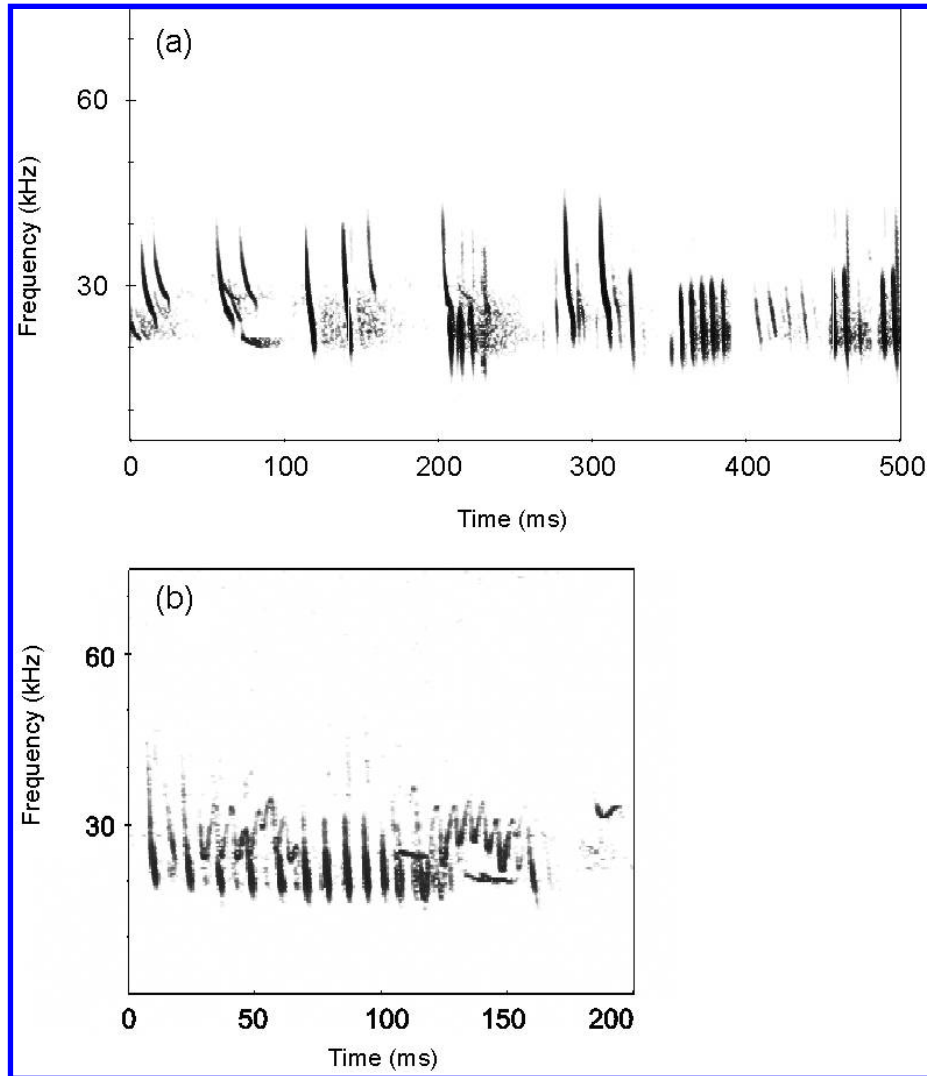
Echolocation call design varies in *T. brasiliensis* with respect to social context (i.e., number of bats flying together). When flying with conspecifics, *T. brasiliensis* use a wider range of frequencies than when flying alone, and social calls are often found mixed with echolocation calls. It remains to be empirically demonstrated whether changes in echoloca-

tion call features of the magnitude we observed reflect jamming avoidance, enhancement of communication, or both. Molossids, such as *T. brasiliensis*, are fast fliers with high aspect ratios and high wing loadings (Norberg and Rayner 1987). In the absence of positional information about nearby conspecifics, which could be encoded by changes in echolocation calls, bats might suffer from more mid-air collisions. Our data showed that *T. brasiliensis* changed its call frequency in the presence of conspecifics so that the disparity between bats flying together (actual pairs) was significantly greater than the disparity when the calls used by two bats flying alone were randomly paired (virtual pairs). Regardless of the underlying mechanism for this pattern, differences in call frequencies used by bats flying together should alleviate some interference associated with using the same frequencies in the same air space (Habersetzer 1981). Our finding is especially satisfying since we found more variation in call peak frequencies used by two bats flying concurrently in the same airspace than we did between two bats flying in two different locations; locations which differed at least somewhat in habitat structure. The high mobility of individual *T. brasiliensis* (>50 km to foraging sites; Wilkins 1989) might explain the lack of significant differences in echolocation calls between sites in Mexico City.

In some species of aerial-feeding bats, playback presentations of feeding buzzes attract conspecifics (Barclay 1982; Balcombe and Fenton 1988), because feeding buzzes indicate the presence of prey (Reddy and Fenton 2003). Playbacks of simulated feeding buzzes increase general levels of activity by foraging *T. brasiliensis* (G.F. McCracken, personal observation). Thus, higher incidences of conspecific interference at feeding sites where jamming might have the most detrimental effect on individual foraging success were expected to occur when individuals converged on rich patches of prey. The qualities that make echolocation and other forms of environmental sounding (see Dusenbery 1992) so remarkable should also make these systems more susceptible to eavesdropping and increased levels of intraspecific competition. Therefore, a less tenable third alternative to jamming avoidance and communication may be that individual bats change their peak frequency to reduce the range at which echoes returning from their own calls can be detected by conspecifics, thereby reducing opportunities for eavesdropping. However, the fact that little brown bats (*Myotis lucifugus* (LeConte, 1831)) use the echolocation calls of big brown bats (*Eptesicus fuscus* (Beauvois, 1796)), which are typically more than 10 kHz lower in peak frequency (Barclay 1982), argues against this possibility.

Our recordings suggest a continuum in call features between echolocation and social calls (Figs. 1 and 2), indicating that the distinction between these call types may not be fixed. Pfalzer and Kusch (2003) described social calls recorded from 16 species of European vespertilionids and

Fig. 2. Spectrograms (1024 point FFT) illustrating the most common patterns exhibited in the social calls of *T. brasiliensis*.



identified at least four types by call complexity. The vesperilionid social calls appeared to function in situations that included mother–infant recognition, mate attraction, aggression or warning to conspecifics, and distress responses. The calls we observed seem to fit best into the categories these authors identified as “repeated trills” and “song-like calls”, more frequently recorded in bats subjected to different kinds of severe interference or when foraging in groups (Pfalzer and Kusch 2003). Although this suggests that song-like calls could have similar functions in *T. brasiliensis*, the actual role of the observed social calls remains to be tested in more controlled experiments. To be even-handed, there also is the possibility that the changes in peak frequency which we found in echolocation calls are neither jamming avoidance nor air traffic control, but serve another and as yet undetermined communicative function.

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