

# Syllable acoustics, temporal patterns, and call composition vary with behavioral context in Mexican free-tailed bats

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Recent research has shown that some bat species have rich vocal repertoires with diverse syllable acoustics. Few studies, however, have compared vocalizations across different behavioral contexts or examined the temporal emission patterns of vocalizations. In this paper, a comprehensive examination of the vocal repertoire of Mexican free-tailed bats, *T. brasiliensis*, is presented. Syllable acoustics and temporal emission patterns for 16 types of vocalizations including courtship song revealed three main findings. First, although in some cases syllables are unique to specific calls, other syllables are shared among different calls. Second, entire calls associated with one behavior can be embedded into more complex vocalizations used in entirely different behavioral contexts. Third, when different calls are composed of similar syllables, distinctive temporal emission patterns may facilitate call recognition. These results indicate that syllable acoustics alone do not likely provide enough information for call recognition; rather, the acoustic context and temporal emission patterns of vocalizations may affect meaning. © 2008 Acoustical Society of America.

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## I. INTRODUCTION

Extensive research on vocal communication has been conducted on anurans, birds, cetaceans, and nonhuman primates (Todt *et al.*, 1988; Tyack and Clark, 2000; Ryan, 2001; Marler, 2004). Less attention has been given to bats although several studies report various types of communication calls. These include infant isolation calls (e.g., Gould *et al.*, 1973; Gelfand and McCracken, 1986), maternal directives (Esser and Schmidt, 1989; Balcombe and McCracken, 1992), mating songs (Barlow and Jones, 1997; Davidson and Wilkinson, 2002; Behr and von Helversen, 2004), distress calls (Russ *et al.*, 1998; Russ *et al.*, 2004), and group foraging calls (Wilkinson and Boughman, 1998). A handful of studies have also examined multiple vocalizations within species. These studies have revealed rich repertoires (Barclay *et al.*, 1979; Porter, 1979; Kanwal *et al.*, 1994; Pfalzer and Kusch, 2003; Ma *et al.*, 2006; Melendez *et al.*, 2006), including rules for syllable combinations (Kanwal *et al.*, 1994). Vocalizations can be quite intricate (Behr and von Helversen, 2004), and some species are capable of vocal learning (Esser, 1994; Boughman, 1998). Thus, bats are an intriguing taxon

for vocal communication research but studies that incorporate behavioral and vocal diversities within a species are rare.

Examining multiple vocalizations and corresponding behaviors within a species not only provides an overview of vocal diversity but also permits comparisons of acoustic features across different behavioral contexts. If vocalizations are correlated with different behavioral contexts, they likely have different meanings that should be reflected in their acoustics. Calls are usually identified and described by the acoustic features of individual elements (e.g., Cleveland and Snowdon, 1982; Seddon *et al.*, 2002; Range and Fischer, 2004), which we will refer to as syllables. Syllable acoustics can also vary with and provide information on identity at the individual (Cheney and Seyfarth, 1980; Hauser, 1991; Bohn *et al.*, 2007), group (Boughman, 1997), or family (Gouzoules and Gouzoules, 1990) level.

Although syllable acoustics may be an important means for conveying information, other features of vocalizations may be equally significant. There are at least four other ways in which vocalizations have varied with behavioral context or elicited differential responses from receivers. (1) The temporal distribution of syllable emissions. Most salient is whether syllables are emitted in distinct clusters (i.e., calls are multisyllabic) or emitted singly (i.e., calls are monosyllabic; Cleveland and Snowdon, 1982). (2) The rate at which syllables are emitted over time (i.e., call rate; Hauser, 1998;

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Ghazanfar *et al.*, 2002; Searby *et al.*, 2004). (3) The number of syllables per call (Ghazanfar *et al.*, 2002). (4) Acoustic context, that is, whether and how syllables are combined (Cleveland and Snowden, 1982; Robinson, 1984; Crockford and Boesch, 2005). The first two features, temporal distribution and call rate, relate to temporal emission patterns whereas the second two features, the number of elements per call and acoustic context, relate to call composition. Both temporal emission patterns and call composition have received much less attention than syllable acoustics, particularly in bats, even though they may be perceptually salient and an integral component of vocal communication.

Here, we examine the vocal repertoire of Mexican free-tailed bats and test whether syllable acoustics, temporal emission patterns, and/or call composition vary among vocalizations emitted in different behavioral contexts. We describe 16 vocalizations associated with particular behaviors, including complex territorial-courtship song produced by males during the mating season. For each vocalization, we examine the distribution of syllable emissions over time and use a quantitative analysis to determine whether vocalizations consist of single syllables or whether multiple syllables are emitted as units. Finally, we determine whether different calls are distinguishable based on syllable acoustics, temporal emission patterns, or call composition features.

## II. METHODS

### A. Study site and animals

This study was conducted on a captive colony of approximately 60 *T. brasiliensis*. The colony has been maintained by Schmidt-French in Austin, TX, for a period of ten years, and the identity, sex, and history for each individual have been documented. Schmidt-French could identify individuals by sight or after examination. Bats were housed in a wooden structure measuring 4.9 m (length)  $\times$  3.7 m (width)  $\times$  3.7 m (height). Two windows allowed filtered sunlight to enter. Humidity was maintained at 60% or above and temperatures varied in the building from approximately 22 to 26 °C. Cloth-covered heating pads placed in cages during evening hours provided bats with the option of accessing temperatures reaching 29 °C. The bats roosted in fabric pouches positioned along the walls and ceilings of open wooden cages and had access to the entire building. Bats had continual access to water and beetle larvae (*Tenebrio molitor*), and were also offered a blended mixture of larvae, baby food, and vitamin supplements in the evening (Lollar and Schmidt-French, 2002).

### B. Acoustic recordings

We observed behaviors and recorded vocalizations during the late evening (2200–0100 h) when the bats were most active. The bats were accustomed to the building being well lit during this time allowing direct observation and recording of behaviors onto a digital camcorder (Sony DCR-TRV-460). Behaviors that occurred inside roosting pouches were recorded using a Night Owl Cam (Model NI 201), a complementary metal oxide semiconductor camera with infrared and microphone (Birdhouse Spy). In order to compare social

vocalizations with echolocation calls, we recorded echolocation calls from each of the three bats while they flew in the colony room. Vocalizations were recorded using a  $\frac{1}{4}$  in. microphone (Brüel and Kjær type 4939) and a custom-made amplifier. In 2003, signals were recorded into a custom-made digital time expander. The time expander recorded a maximum of 10 s at 16 bits that was played onto a computer at a sample rate of 44.1 kHz. In 2004 and 2005, calls were recorded directly onto a computer at a sample rate of 300 kHz using a high-speed data acquisition card (National Instruments, NI PCI 6251 M Series, Austin, TX) and AVISOFT software (version 2.97, Avisoft Bioacoustics, Berlin, Germany). Both systems allowed recordings up to 150 kHz, well above the frequency content of vocalizations. For analyses, we only examined recordings where the identity of the caller was known and the corresponding behavior was observed. After examining vocalizations and recordings, we further restricted our analyses to those vocalizations that were unambiguously correlated with specific behaviors and observed in at least three individuals.

### C. Terminology

We used the following terms to describe vocalizations:

*Syllable*. The smallest acoustic unit of a vocalization in this study and equivalent to one continuous emission surrounded by silence (Kroodsma, 1977; Kanwal *et al.*, 1994).

*Call*. The simplest emission of a vocalization. Calls can be composed of single syllables or groups of syllables. For all vocalizations except for song, we use quantitative methods (see Sec. II D) to determine what constitutes a call. If syllables are emitted singly, then each syllable is a *monosyllabic* call. Alternatively, if multiple syllables are always emitted together then the group of syllables is a *multisyllabic* call.

*Bout*. A group of calls.

*Song*. Vocalizations emitted by males during the mating season that have multiple types of syllables and phrases (Catchpole and Slater, 1995; Marler and Slabbekoorn, 2004).

*Phrase*. A combination of one or more types of syllables that may be repeated in a song (Kroodsma, 1977; Marler and Slabbekoorn, 2004). *Simple phrases* are composed of one type of syllable. *Complex phrases* are composed of different types of syllables (similar to a “note complex” phrase in birds, Kroodsma, 1977; Marler and Slabbekoorn, 2004).

### D. Temporal analysis

We used temporal analyses to classify calls as mono- or multisyllabic and to demarcate intracall intervals from intercall intervals. For all recordings, we normalized amplitudes and determined the beginning and end times of syllables on oscillograms. We tested whether syllables were distributed randomly across time by dividing recordings into equal time intervals and then comparing the distribution of the number of syllables per time interval with a Poisson distribution. Time interval lengths varied by call but were selected so that the mean number of syllables per interval was consistently between 1 and 2 (Zar, 1984). If the temporal distribution of syllables was significantly different than random, we classi-

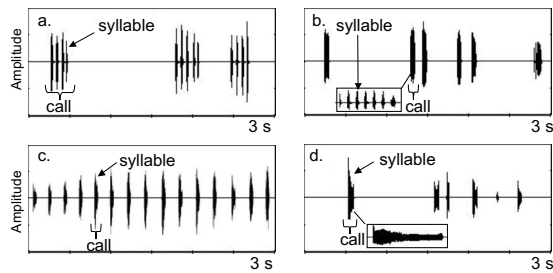


FIG. 1. Temporal emission patterns of *Tadarida* vocalizations. (a) and (b) are multisyllabic calls with clumped syllable distributions and syllables are never emitted singly. (c) Monosyllabic calls with a uniform syllable distribution and (d) monosyllabic calls with a random distribution. (a) Maternal directives, (b) irritation calls, (c) mounting calls, and (d) marking calls.

fied the distribution as clumped if the variance was greater than the mean, or uniform if the variance was less than the mean (Zar, 1984). We considered calls multisyllabic if syllables were emitted in a clumped manner where each “clump” represented a call [Figs. 1(a) and 1(b)], and monosyllabic if syllables were emitted randomly or uniformly [Figs. 1(c) and 1(d)]. In order to avoid biasing results by including long intervals of silence, we did not use intervals of 4000 ms or more (32 of 5726 intervals).

Next, for calls with clumped distributions, we used bout analyses (Sibly *et al.*, 1990) to determine thresholds between intercall intervals and intracall intervals (intervals between syllables within calls). For each call type, we calculated the log frequency of intervals per unit time across the range of interval lengths. We used nonlinear regression (PROC NLIN, SAS Institute, Cary, NC) to fit a two-process model to the data, where the fast process represented syllable intervals and the slow process represented call intervals (Sibly *et al.*, 1990). Once intercall thresholds were established, we calculated the number of syllables per call for each call type.

### E. Syllable measurements

We measured acoustic features for syllables from each call and for four types of syllables found in song. We randomly selected five syllables from three randomly selected bats for each syllable type. We band-pass filtered syllables between 1 and 100 kHz and normalized amplitudes by dividing each signal by its peak amplitude. Syllables were measured using SASLAB PRO (version 4.39, Avisoft Bioacoustics). We measured syllable duration (*dur*) from oscillograms. We measured five frequency characteristics of the fundamental frequency, which was usually dominant: peak frequency ( $f_{\text{peak}}$ ), beginning frequency ( $f_{\text{beg}}$ ), end frequency ( $f_{\text{end}}$ ), maximum frequency ( $f_{\text{max}}$ ), and minimum frequency ( $f_{\text{min}}$ ). Peak frequency ( $f_{\text{peak}}$ ) was measured from power spectrums and the other frequency variables were measured from spectral contours. Click syllables and protest syllables were measured differently. Clicks were of such short duration (<1 ms) that we could not construct meaningful spectral contours and so we did not measure  $f_{\text{beg}}$  and  $f_{\text{end}}$ , and we measured  $f_{\text{min}}$  and  $f_{\text{max}}$  on power spectrums at  $-20$  dB below peak frequency. Protest syllables had most energy at harmonics above the fundamental and the fundamental often did not clearly show the shape of the syllables. For these calls, we

measured  $f_{\text{peak}}$  at the fundamental but measured the remaining four frequency variables from the dominant harmonic. For descriptive purposes alone, we also calculated call bandwidths as  $\log_2(f_{\text{max}}/f_{\text{min}})$ .

### F. Syllable acoustic analysis

For syllable analyses, our goals were to (1) describe syllable acoustic structure and variation and to (2) determine whether syllable acoustics differed when syllables were incorporated into different calls or song. First, we visually examined syllables and observed that they fell into three acoustic groups: clicks, downward frequency-modulated (FM) sweeps (down FMs), and long syllables. We used discriminant function analysis to confirm these groupings using  $f_{\text{peak}}$  and *dur*, as these were the only variables measured consistently across all syllables. Next, for each group, we screened variables for high correlations. We removed highly correlated measurements. We excluded maximum ( $f_{\text{max}}$ ) and minimum ( $f_{\text{min}}$ ) frequencies in analyses for down FMs because they were highly correlated with beginning ( $f_{\text{beg}}$ ) and end ( $f_{\text{end}}$ ) frequencies, respectively ( $r=0.99$ ,  $p<0.0001$ ,  $N=115$  for both pairs of variables). Next, within each of the three groups, we used a multiple analysis of variance (MANOVA) with call as a factor and bat nested within call as a random factor to determine if syllables differed among calls or bats (PROC GLM, SAS). For acoustic groups that showed significant differences between calls, we performed discriminant function analyses to determine which syllables varied among different calls (PROC DISCRIM, SAS). For all discriminant function analyses and MANOVAs, we tested for normality using Shapiro–Wilk tests and, if necessary, used  $\log_{10}$  and square-root transformations to meet normality requirements. Misclassification rates were calculated using leave-one-out cross-validation (PROC DISCRIM, SAS). We present figures of canonical functions with eigenvalues greater than 1. All temporal variables are presented in ms and all frequency variables in kHz.

### G. Temporal emissions and call composition

In the next analysis, we determined whether calls that were composed of similar syllables differed in their temporal emission patterns or call composition features. First, we compared the distribution of syllable emissions. Multisyllabic calls (calls with clumped distributions) were considered different and discriminable from monosyllabic calls (calls with random or uniform distributions). Second, we considered the acoustic context of vocalizations and considered cases where syllables were embedded in complex phrases in song as discriminable from other calls. Third, we compared syllable emission rates. For monosyllabic calls, we tested whether call rates (calls/s) differed across calls using analysis of variance (ANOVA) and Tukey tests (Zar, 1984). Call rates were calculated for each recording but there were not enough recordings for each bat to include it as a nested factor. For multisyllabic calls, we used ANOVAs with bat as a nested random factor and Tukey tests to compare the interval between syllables within calls. Finally, we compared the number of syllables per call for multisyllabic calls using ANO-

VAs with bat as a nested random factor and Tukey tests. All data are presented as means  $\pm$  standard error of the mean unless stated otherwise.

### III. RESULTS

#### A. Vocalizations and behaviors

We identified 16 vocalizations associated with different behaviors that we divided into six categories: (1) mating, (2) parent-offspring, (3) antagonistic, (4) social, (5) human interaction, and (6) flight. Below, we briefly describe the behavioral context, acoustic structure, and temporal emission pattern of each vocalization. We also include sample sizes where *bats* and *records* refer to the number of bats we recorded from and the total number of recordings, respectively.

##### 1. Mating

These calls were only emitted by reproductively active adults during the mating season. Most of the year males and females roosted together and males did not establish individual territories nor did they exhibit territorial behavior. In contrast, during the mating season, from January through May, dominant males (approximately 50% of males in the colony) roosted alone in one of the handmade pouches. Each roosting pouch was a dominant male's territory where he actively recruited reproductively active females and fought encroaching males.

**Herding calls.** These calls were produced during a highly stereotyped behavior, while a male forcefully pushed one or more females with his muzzle or wing into a cluster inside his territory [Fig. 2(a), bats=5, records=14]. Herding calls were multisyllabic (Table I) and consisted of three to ten downward FM sweep syllables (Table II). In approximately 35% of the 116 calls we recorded, syllables were emitted continuously forming sinusoidlike calls [Fig. 2(a)]. In many cases, the down FM sweep calls would transition to sinusoidlike calls within a bout of herding calls.

**Marking calls.** Dominant males emitted this call while rubbing their faces, gular glands, and penis on the surfaces of their territories [Fig. 2(b), bats=3, records=25]. Males also emitted marking calls over long periods of time (30 min or more) while relatively inactive on their territories, which suggests that marking calls could function in territory maintenance. Marking calls were emitted randomly and considered monosyllabic [Table I and Figs. 1(d) and 2(b)]. Syllables were long (durations up to 80 ms) and low in frequency (4–11 kHz) with highly variable spectrotemporal features.

**Mounting calls.** Mounting calls were produced during a highly stereotyped behavior. A male would attempt to mount a female, and produce these calls as he forcefully pushed his muzzle repeatedly between her shoulders [Fig. 2(c), bat=8, records=17]. These calls may be associated with dominance, as males never copulated during these encounters and sometimes performed similar behaviors when interacting with juvenile males. Mounting calls were monosyllabic and emitted at regular intervals [Table I and Figs. 1(c) and 2(c)]. Syllables were multiharmonic and relatively constant frequency (bandwidths less than 0.5 octaves).

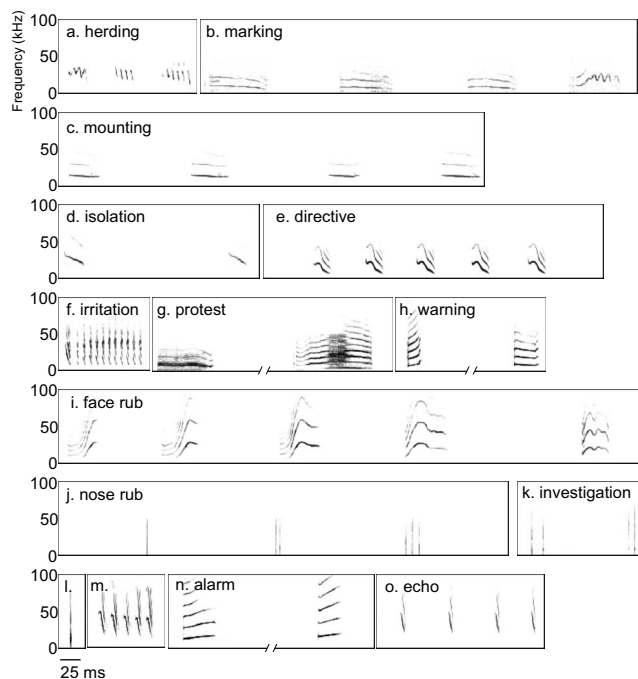


FIG. 2. Spectrograms of calls emitted by *T. brasiliensis*. (a) Three herding calls, (b) four marking calls [also see Fig. 1(d)], (c) four mounting calls [also see Fig. 1(c)], (d) three isolation calls, (e) one directive call [also see Fig. 1(a)], (f) one irritation call [also see Fig. 1(b)], (g) two protest calls (each call is from a different bat), (h) two warning calls (each call is from a different bat), (i) face-rubbing call, (j) nose-rubbing call, (k) investigation clicks, (l) food click, (m) food solicitation call, (n) two alarm calls (each call is from a different bat), and (o) four echolocation calls.

**Territorial/courtship songs.** Most males that established territories (approximately 75%) produced territorial/courtship song (here forth referred to as “song”) when reproductively active females or dominant males approached their territories, or when other males sang. While singing to females, males marked their territories with secretions from their gular glands, anus, and penis, and performed wing-flapping displays (French and Lollar, 1998). Alternatively, if another male intruded on the established territory of a dominant male, the territorial male sang and often chased the intruding male away.

Songs were the most complex vocalizations we recorded and were composed of up to three principal phrases: chirps, trills, and buzzes (Fig. 3, bats=16, records=116). Chirp phrases were complex phrases since they were composed of two types of syllables: “type A” syllables and “type B” syllables [Fig. 3(b)]. Each chirp began with 1–18 repetitions of type A syllables and terminated with a single type B syllable. Type A syllables were brief, 3–7 ms downward FM sweeps. The chirp phrase was repeated 1–36 times in each song (median=7,  $N=171$  songs). Type B syllables were more complex in that they usually had both upward and downward FM components and were longer in duration (14–20 ms, see Sec. III B). In addition to chirps, 60% of songs also contained trills, buzzes, or both phrases [ $N=171$  songs, Figs. 3(c) and 3(d)]. Both trills and buzzes were simple phrases composed of a series of rapidly repeated downward FM sweep syllables.

TABLE I. Results of chi-squared tests on the distribution of syllables over time.

Call <sup>a</sup>	Chi-squared	df	P	N Syllables	Variance/mean	Distribution
Alarm	0.9	3	0.82	103	1.0	Random
Echo	70.4	4	<0.0001	451	0.5	Uniform
Food	610.1	4	<0.0001	403	2.66	Clumped
Herding	186.3	4	<0.0001	448	1.59	Clumped
Isolation	18.7	3	0.0003	553	0.8	Uniform
Irritation	1508.9	5	<0.0001	1203	4.5	Clumped
Marking	2.2	3	0.53	109	0.8	Random
Directive	259.4	4	<0.0001	261	2.9	Clumped
Mounting	44.1	3	<0.0001	120	0.5	Uniform
Protest	4.1	4	0.39	153	0.9	Random
Question	5.9	3	0.12	96	1.1	Random
Warning	77.2	4	<0.0001	249	0.4	Uniform

Food=food solicitation, isolation=infant isolation, and directive=maternal directive. Temporal analyses were not performed on anticipation clicks, nose-rubbing calls, or face-rubbing calls because there were no intercall data. Anticipation clicks were always emitted singly and the other two calls were multisyllabic but only one call was ever recorded at a time.

## 2. Parent-Offspring

These vocalizations were only produced by lactating females and their young.

*Infant isolation calls.* Neonates emitted isolation calls immediately after birth and continued to emit these calls throughout development. Pups called when they were isolated or when milk was no longer visible in their stomachs. Infant isolation calls were monosyllabic and although sometimes emitted alone; they were also produced in long trains at relatively constant intervals resulting in a uniform distribution [Table I and Fig. 2(d), bats=4, records=14]. Isolation calls had variable FM patterns that were often simpler and with smaller bandwidths (usually less than one octave) than maternal directives (see below). Previous research has shown that isolation calls are individually distinctive (Gelfand and McCracken, 1986) and that females can discriminate isolation calls from their own pups (Balcombe, 1990).

*Maternal directive calls.* Maternal directives were emitted throughout pup development when females approached

pups or in response to pups' isolation calls. Maternal directive calls were multisyllabic (Table I) with 3–11 syllables per call [Table II and Figs. 1(a) and 2(e), bats=7, records=22]. This call showed a stereotyped number of syllables as demonstrated by a low coefficient of variation (Table II). Directive syllables also had complex FM patterns, often with both upward and downward components that spanned up to two octaves. Previous research has shown that these calls are individually distinctive (Balcombe and McCracken, 1992).

## 3. Antagonistic

Both males and females, regardless of reproductive status, emitted these calls during agonistic interactions.

*Irritation calls.* Bats produced these calls when (1) they were jostled by another bat in the roost or (2) when disturbed by a handler. Bats would sometimes push their muzzles into or head-butt another bat while producing this call. In response to irritation calls, bats would often emit protest calls or bare their teeth and emit warning calls. Irritation calls

TABLE II. Results of bout analyses for multisyllabic calls. R-squared values for the two-process nonlinear models, intercall threshold from two-process models, median, range, and coefficient of variation (CV = standard deviation/mean) of the number of syllables per call, the interval between syllables within calls (mean ± SE), and sample sizes. Nonlinear models were not fitted to face-rubbing and nose-rubbing calls because we did not have intercall interval data (see text).

Call <sup>a</sup>	R <sup>2</sup>	Intercall threshold (ms)	Median syllables	Range syllables	CV <sup>b</sup>	Syllable interval (ms)	N calls, N intervals
Face rub	...	...	6	4–24	0.64	126.1 ± 6.6	25, 192
Food	0.91 <sup>c</sup>	22	3	2–11	0.38	10.6 ± 0.2	153, 291
Herding	0.89 <sup>c</sup>	11.5	4	3–10	0.36	3.2 ± 0.1	117, 436
Irritation	0.95 <sup>c</sup>	28	5	3–15	0.43	8.7 ± 0.1	237, 1138
Directive	0.83 <sup>c</sup>	168	5	3–11	0.29	59.2 ± 1.4	65, 277
Nose rub	...	...	13	5–28	0.49	31.8 ± 2.4	19, 263
Trill	...	...	4	2–10	0.33	3.7 ± 0.1	118, 289
Buzz	...	...	23	5–44	0.45	4.4 ± 0.3	111, 2085

Food=food solicitation, directive=maternal directive, and trill and buzz are from song. CV=coefficient of variation=(standard deviation/mean) of the number of syllables/call. P<0.0001.

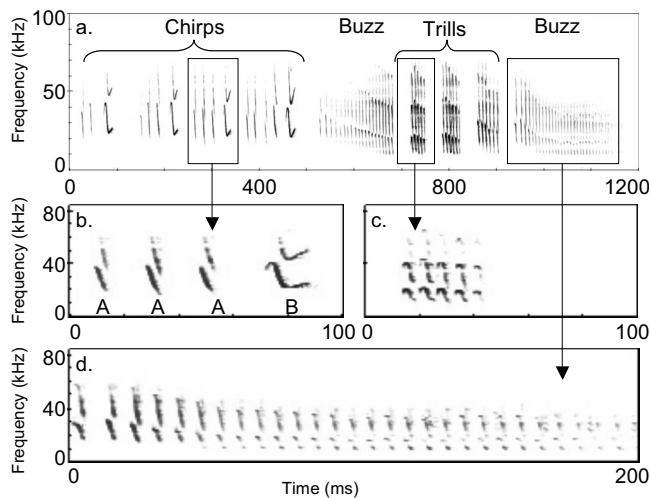


FIG. 3. Territorial/courtship song. (a) One complete song showing the three types of phrases: chirp, buzz, and trill. (b) Expanded section of a chirp, which has two types of syllables: types A and B. (c) Expanded section of a trill. (d) Expanded section of a buzz.

were multisyllabic [Table I and Fig. 1(b), bats=14, records=28], with between 3 and 15 short downward FM sweep syllables per call [Table II and Fig. 2(f)].

**Protest calls.** We recorded these calls in three situations: when a female struggled to escape a male that was attempting to mount her, when a bat was shoved or swatted by another bat, and when a bat was in discomfort from human handling. When bats emitted protest calls, they behaved submissively; they struggled, retreated, or froze with their bodies flattened against the roost surface. Protest calls were monosyllabic (Table I) and emitted singly or in bouts. Of all vocalizations, protest syllables were the longest (durations up to 105 ms) and had the lowest frequencies [fundamental frequencies between 1 and 2 kHz, Fig. 2(g), bats=14, records=18]. They had variable FM components with bandwidths of the dominant harmonic of up to one octave. Protest syllables were squeal-like in that energy was spread across many harmonics and there were often subharmonics. Dominant harmonics similar to formants occurred at higher frequencies than the fundamental.

**Warning calls.** We recorded warning calls during three types of situations: when a male entered another male's territory during the mating season, during physical altercations with other bats in the roost, or when in distress from human handling. While emitting these calls, bats would use their heads to shove or used their wings to swat other bats. Bats would respond to warning calls with either aggressive displays (baring teeth and head bobbing) or they would produce protest calls and retreat. Warning calls were monosyllabic and although frequently emitted alone, they were also emitted in long trains at relatively constant intervals resulting in a uniform distribution [Table I and Fig. 2(h), bats=11, records=25]. Syllables were loud and relatively constant frequency with bandwidths less than 0.5 octaves.

#### 4. Social

Both males and females, regardless of reproductive status, emitted these calls while roosting with conspecifics. They were not associated with agonistic interactions.

**Face-rubbing calls.** Bats emitted face-rubbing calls during a highly stereotyped behavioral sequence. They hopped a few centimeters towards another bat, rubbed their muzzles across the body of the bat, and sometimes tapped the other bat with a folded wing. Face-rubbing calls were multisyllabic since syllables were never emitted alone. We never recorded more than one call at a time with up to 5 min recordings. Consequently, we had no intercall intervals to perform temporal distribution patterns. Face-rubbing calls were composed of 4–24 syllables, but the number of syllables per call was highly variable compared to the other vocalizations (Table II, coefficient of variation=0.64). The structure of face-rubbing syllables was also highly variable [Fig. 2(i), bats=9, records=23]. Spectrotemporal patterns included both upward and downward FM components. Some syllables were relatively constant frequency with bandwidths less than 0.25 octaves, whereas others had bandwidths of up to 3 octaves.

**Nose-rubbing calls.** These calls were also produced during a specific behavior, while a bat gently rubbed its muzzle against another bat's muzzle. They appeared to possibly function as a greeting because callers usually directed them at bats as they first entered the roost. Nose-rubbing vocalizations were always emitted as multisyllabic calls. We never recorded more than one call at a time (for up to 5 min periods). Thus, like face-rubbing calls, we had no intercall intervals for temporal pattern analyses. Nose-rubbing calls were comprised of between 5 and 28 clicks [Fig. 2(j), bats=9, records=21].

**Investigation clicks.** We recorded these clicks when a bat approached a novel stimulus at a roost pouch such as an entering bat or human. Investigation clicks were emitted randomly and considered monosyllabic [Table I and Fig. 2(k), bats=6, records=9]. They were similar to other click syllables.

#### 5. Human interaction

All bats (males, females, and juveniles) produced these calls during interactions with human handlers.

**Food clicks.** Food clicks were only produced while the handler prepared food but were not accompanied by any specific behaviors. They were similar to other click syllables; however, they were louder and always emitted singly; hence, we did not perform temporal analyses [Fig. 2(l), bats=15, records=17].

**Food solicitation calls.** Bats emitted these calls during or immediately prior to feeding time. While producing these calls, bats approached the handler, sometimes hopping repeatedly and flapping their wings. Food solicitation calls were multisyllabic [Table I and Fig. 2(m), bats=8, records=18] and comprised of 2–11 (Table II) downward FM sweeps.

**Alarm calls.** These calls were associated with high levels of aggression and we only recorded these vocalizations from rabid bats or when wild bats were handled for the first time in captivity. Calling bats rose up on straightened elbows, jerked their bodies, and bared their teeth. Alarm calls were monosyllabic and emitted alone or in bouts [Table I and Fig.

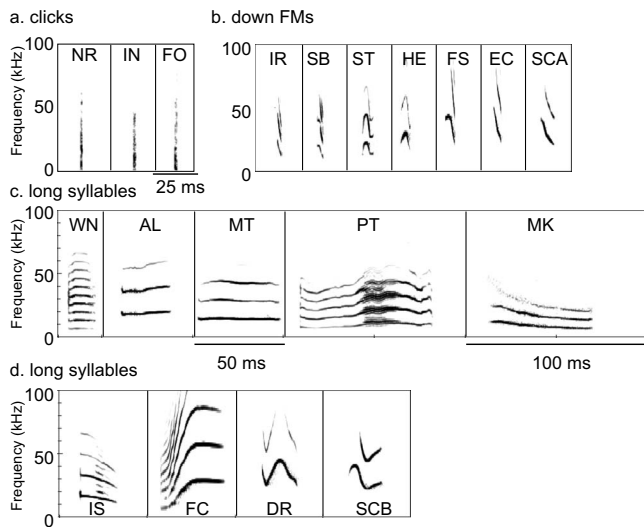


FIG. 4. Spectrograms of syllable types. (a) Clicks, NR=nose rubbing, IN=investigation, and FO=food click. (b) Brief downward frequency modulated syllables (down FMs), IR=irritation, SB=song buzz, ST=song trill, HE=herding, FS=food solicitation, EC=echolocation, and SCA=song chirp type A. [(c) and (d)] Long syllables, WN=warning, AL=alarm, MT=mounting, PT=protest, MK=marking, IS=isolation, FC=face rubbing, DR=directive, and SCB=song chirp type B.

2(n), bats=3, records=10]. Syllables were high amplitude and constant frequency (bandwidths less than 0.3 octaves).

## 6. Flight

In order to compare social vocalizations with echolocation signals, we recorded calls from three bats as they flew inside the barn.

**Echolocation calls.** Echolocation calls were monosyllabic and often emitted continuously [Table I and Fig. 2(o), bats=3, records=6]. They were short downward FM sweeps.

## B. Syllable acoustics and temporal patterns

In this section, we (1) examine the acoustic features of syllables from each call, (2) determine whether each of the different calls is composed of a unique syllable, and (3) examine temporal patterns and call composition of calls that share common syllables. We examined the acoustic structure of 19 types of syllables. One for each call type and four types of syllables from song: type A and type B syllables in chirps, trill syllables, and buzz syllables.

First, we found that syllables fit into three distinct acoustic groups: (1) clicks, (2) down FMs, and (3) long syllables (Fig. 4). Discriminant function analysis confirmed these categories with 100% correct classification [Wilk's lambda=0.067,  $df=4, 562$ ,  $P<0.0001$ , Fig. 5(a)]. Duration was the most distinctive feature of these groups. Clicks were less than 1 ms, down FMs ranged between 1 and 8 ms, and long syllables ranged between 8 and 106 ms. With the exception of song, calls were composed of syllables from only one major acoustic group. For example, the only syllables in nose-rubbing calls were clicks while the syllables in irritation and food solicitation calls were all down FMs (Figs. 2 and 4). Since calls composed of syllables from different acoustic groups, clicks, down FMs, or long syllables should

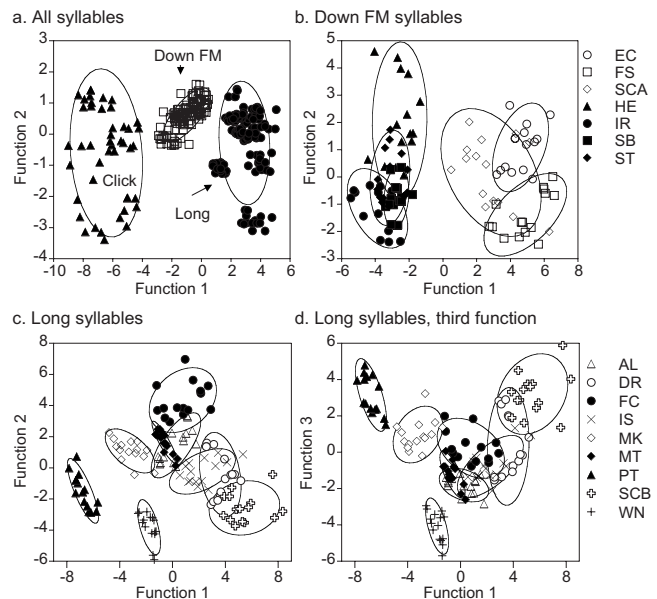


FIG. 5. Canonical functions from discriminant function analyses. (a) All syllables fell into three distinct types. Function 1 was correlated with duration ( $r=0.99$ ) and function 2 was correlated with peak frequency ( $r=0.99$ ). The lines depict 80% normal bivariate density ellipses. (b) Down FM syllables. Function 1 was correlated with all variables. Function 2 was correlated with end and peak frequencies. We recognized two syllable subgroups: The first subgroup consisted of echolocation (EC), escape (ES), food solicitation (FS), and song chirp type A (SCA) syllables (open symbols) and the second subgroup consisted of irritation (IR), song buzz (SB), herding (HE), and song trill (ST) syllables (filled symbols). [(c) and (d)] Long syllables. Function 1 was correlated with frequency features, function 2 was most correlated with duration (c), and function 3 was most correlated with maximum frequency (d). AL=alarm, DR=maternal directive, FC=face rubbing, IS=isolation, MK=marking, MT=mounting, PT=protest, and SCB=song chirp type B. The lines depict 80% normal bivariate density ellipses.

be highly distinguishable, we determined whether calls in each acoustic group can be distinguished by other features, specifically by syllable acoustics, temporal patterns, or call composition.

### 1. Clicks

The four acoustic features we measured (dur,  $f_{min}$ ,  $f_{max}$ , and peak) did not differ between click calls (MANOVA; Wilk's lambda=0.15,  $df=8, 6$ ;  $P=0.43$ ; mean  $\pm$  SE; dur:  $0.34 \pm 0.04$  ms,  $f_{min}=4.2 \pm 0.8$  kHz,  $f_{max}=32.3 \pm 2.4$  kHz, peak= $15.0 \pm 1.9$ ). Therefore, the various calls composed solely of clicks are acoustically indistinguishable by the clicks themselves. However, the distribution of syllable emissions did differ between click calls. Anticipation clicks were only emitted singly, question clicks were emitted randomly, and nose-rubbing calls were the only multisyllabic calls where clicks were always emitted in distinct groups.

### 2. Down FMs

We examined four acoustic features of syllables from down FM calls (Table III). We found that syllables differed among calls (MANOVA: Wilk's lambda=0.001,  $df=24, 39$ ,  $P<0.0001$ ) and bats (Wilk's lambda=0.08,  $df=56, 317$ ,  $P<0.0001$ ). In order to examine which calls could be distinguished by syllable acoustics, we performed a discriminant function analysis. This analysis resulted in two canonical

TABLE III. Mean  $\pm$  SE of down FM syllable measurements.

Syllable <sup>a</sup>	Code	Subgroup <sup>b</sup>	Temporal feature <sup>c</sup>	dur	$f_{\text{beg}}$	$f_{\text{end}}$	$f_{\text{peak}}$
Echo	EC	1	Mono	5.1 $\pm$ 0.2	52.1 $\pm$ 0.9	28.1 $\pm$ 0.9	35.9 $\pm$ 1.1
Food	FS	1	Multi	5.9 $\pm$ 0.3	49.9 $\pm$ 1.4	22.0 $\pm$ 1.0	27.9 $\pm$ 1.1
Song A	SCA	1	Context	5.0 $\pm$ 0.3	43.9 $\pm$ 1.5	21.0 $\pm$ 0.4	35.0 $\pm$ 2.3
Herding	HE	2	Context	3.2 $\pm$ 0.2	25.5 $\pm$ 1.0	21.6 $\pm$ 1.4	26.8 $\pm$ 1.1
Irritation	IR	2	ISI	2.3 $\pm$ 0.2	18.0 $\pm$ 1.0	11.2 $\pm$ 0.6	13.0 $\pm$ 0.4
Buzz	SB	2	Number	2.9 $\pm$ 0.1	22.2 $\pm$ 0.5	12.4 $\pm$ 0.3	19.5 $\pm$ 1.1
Trill	ST	2	Context	3.4 $\pm$ 0.3	20.7 $\pm$ 0.8	13.6 $\pm$ 0.9	22.2 $\pm$ 0.7

Food=food solicitation, song A=song chirp type A syllable, and buzz and trill are from song.

Discriminant function analysis revealed two acoustic subgroups.

Temporal features that differentiated calls from the same subgroup. Call distribution (mono- or multisyllabic), acoustic context (context), intersyllable interval (ISI), and number of syllables (number).

functions with eigenvalues greater than 1, which together explained 96% of the variation in the four acoustic variables [Fig. 5(b)]. Examination of the distribution of syllables on the first two canonical functions revealed two clusters or “subgroups” of down FM syllables. Subgroup 1 contained echolocation (EC), food solicitation (FS), and song type A syllables (SCA) and subgroup 2 contained herding (HE), irritation (IR), song buzz (SB), and song trill (ST) syllables. Subgroup 1 syllables were generally longer and higher in frequency than subgroup 2 syllables (Table III). Cross-validation resulted in 30 misclassifications (28%), all of which occurred within subgroups ( $N=105$ ). This analysis suggests that syllables from different subgroups should be distinguishable whereas syllables from the same subgroup may be confused with each other.

Next, we examined whether temporal patterns or call composition differed between calls that were composed of syllables from the same down FM subgroup (Table III). For subgroup 1, food solicitation calls were the only multisyllabic calls and hence could be differentiated from echolocation calls and song type A syllables. Type A syllables and echolocation calls differed only by acoustic context; type A syllables were embedded in complex song phrases.

The four vocalizations in subgroup 2, herding calls, irritation calls, song buzz phrases, and song trill phrases, all had similar temporal emission distributions. Herding and irritation calls were both multisyllabic calls (Fig. 2) and we considered song buzz and trill phrases multisyllabic “calls” as well since they were always produced in distinct groups (Fig. 3). We tested whether these calls or phrases differed by the interval between syllables or the number of syllables per call/phrase (Table III). We found that irritation calls had longer intersyllable intervals ( $F_{3,36}=34.0$ ,  $P<0.001$ , Tukey test  $Q=2.69$ ,  $\alpha=0.05$ , Table II) than the other calls/phrases and song buzzes had more syllables ( $F_{3,39}=83.3$ ,  $P<0.0001$ ,  $\log_{10}$ -transformed data; Tukey test,  $Q=2.65$ ,  $\alpha=0.05$ ; Tables II and III). Herding calls and song trills did not differ in either the number of syllables or intersyllable intervals and may only be distinguishable by whether or not they are embedded within songs.

### 3. Long syllables

We examined six acoustic features of long call syllables (Table IV). Long syllable acoustics differed among calls (MANOVA, Wilk’s lambda=0.000 04,  $df=48, 68$ ,  $P$

TABLE IV. Mean  $\pm$  SE of long syllable measurements (ms and kHz).

Syllable <sup>a</sup>	Code	Subgroup <sup>b</sup>	Temporal feature <sup>c</sup>	dur	$f_{\text{beg}}$	$f_{\text{end}}$	$f_{\text{min}}$	$f_{\text{max}}$	$f_{\text{peak}}$
Marking	MK	None	...	58.6 $\pm$ 3.4	9.1 $\pm$ 0.7	6.7 $\pm$ 1.0	6.5 $\pm$ 0.3	9.8 $\pm$ 1.5	7.9 $\pm$ 0.5
Protest	PT	None	...	60.0 $\pm$ 5.1	9.2 $\pm$ 0.6	9.7 $\pm$ 0.8	8.1 $\pm$ 0.6	11.0 $\pm$ 0.8	1.9 $\pm$ 0.1
Warning	WN	None	...	13.4 $\pm$ 0.8	7.2 $\pm$ 0.3	6.6 $\pm$ 0.2	6.3 $\pm$ 0.2	7.3 $\pm$ 0.2	7.0 $\pm$ 0.2
Directive	DR	1	Multi	21.4 $\pm$ 0.6	25.1 $\pm$ 1.4	18.6 $\pm$ 2.1	15.5 $\pm$ 1.4	29.9 $\pm$ 2.4	23.0 $\pm$ 0.4
Isolation	IS	1	Mono	23.3 $\pm$ 0.5	22.6 $\pm$ 1.6	15.3 $\pm$ 1.4	15.1 $\pm$ 1.4	22.8 $\pm$ 1.5	19.4 $\pm$ 1.3
Song B	SCB	1	Context	17.4 $\pm$ 0.5	39.6 $\pm$ 1.4	27.7 $\pm$ 1.1	25.9 $\pm$ 1.4	48.5 $\pm$ 2.5	29.1 $\pm$ 2.4
Alarm	AL	2	Rate	29.4 $\pm$ 1.2	18.8 $\pm$ 1.1	18.8 $\pm$ 1.1	17.8 $\pm$ 1.1	20.0 $\pm$ 1.0	18.5 $\pm$ 1.2
Face rub	FC	2	Multi	50.5 $\pm$ 3.9	13.5 $\pm$ 1.9	23.4 $\pm$ 1.0	12.4 $\pm$ 1.7	25.1 $\pm$ 1.0	23.7 $\pm$ 1.3
Mounting	MT	2	Rate	37.5 $\pm$ 2.0	15.3 $\pm$ 0.5	15.7 $\pm$ 0.4	14.1 $\pm$ 0.4	16.8 $\pm$ 0.3	15.4 $\pm$ 0.2

Directive=maternal directive, isolation=infant isolation, and song B=song chirp type B syllable.

Discriminant function analysis revealed two clusters of calls. Subgroup 1 syllables were longer and had some frequency features that were higher than subgroup 2. “None” refers to syllables that did not overlap with syllables from any other calls.

Temporal features that differentiated calls from the same subgroup. Call distribution (mono- or multisyllabic), acoustic context (context), and call rate (rate).

<0.0001) and bats (Wilk's lambda=0.0009,  $df=108,597$ ,  $P<0.0001$ ). Canonical discrimination resulted in three canonical functions with eigenvalues greater than 1 that together explained 94% of the variation in the six acoustic variables [Figs. 5(c) and 5(d)]. Warning (WN), protest (PT), and marking (MK) syllables did not overlap with syllables from other calls on one or more canonical functions [Figs. 5(c) and 5(d)]. These syllables generally had fundamental frequencies that were lower than the other calls (Table IV). A cross-validation procedure correctly classified all of these syllables. Thus, calls composed of these syllables (WN, PT, and MK) are likely distinguishable from other calls.

The remaining syllables were involved in 26 misclassifications (19% of 135 syllables). All errors occurred within two clusters or subgroups of calls. Subgroup 1 contained maternal directive (DR), song type B (SCB), and isolation (IS) syllables and subgroup 2 included alarm (AL), face-rubbing (FC), and mounting (MT) syllables. Syllables from subgroup 1 were generally briefer and had higher beginning frequencies than subgroup 2 (Table IV). This analysis suggests that calls composed of syllables from different subgroups should be distinguishable, whereas calls composed of syllables from the same subgroup may be confused with each other.

Next, we tested whether calls composed of syllables from the same subgroup differed in temporal emission patterns or call composition (Table IV). Maternal directive calls, isolation calls, and song type B syllables, which comprised subgroup 1, all differed by their emission characteristics. Maternal directive and isolation calls had different temporal emission patterns since maternal directives are multisyllabic and isolation calls are monosyllabic. Song type B syllables differed from the others by their acoustic context because they were embedded within complex phrases in song.

All calls in subgroup 2 (alarm, face-rubbing, and mounting calls) differed in either temporal emission patterns or call composition (Table IV). First, face-rubbing calls differed from the others because they were the only multisyllabic calls in this subgroup. Both alarm and mounting calls were monosyllabic; however, alarm calls were emitted at much lower rates than mounting calls ( $F_{1,32}=23.5$ ,  $P<0.0001$ , alarm calls= $1.0 \pm 0.2$  calls/s, mounting calls= $5.5 \pm 0.6$  calls/s).

#### IV. DISCUSSION

Here, we showed that Mexican free-tailed bats use a rich repertoire of signals for vocal communication. We identified 16 types of vocalizations by the behavioral contexts in which they were emitted. We used quantitative analyses of temporal emissions to determine intercall/intracall boundaries and to define calls as monosyllabic or multisyllabic. We measured spectral and temporal features for syllables from each call and found that many, but not all calls, could be distinguished by the acoustics of their syllables. For those calls that did not have distinctive syllables, most had different temporal emission patterns. Some syllables and phrases were shared be-

tween calls and male song. Below, we discuss the implications of each of the major findings and how they relate to previous studies on vocal communication.

#### A. Vocal diversity

Our results suggest that vocalizations emitted by *T. brasiliensis* are as diverse as other bat species (i.e., *Pteronotus parnelli*, Kanwal *et al.*, 1994; *Rhinolophus ferrumequinum*, Ma *et al.*, 2006; *Saccopteryx bilineata*, Davidson and Wilkinson, 2002). We found that *T. brasiliensis* use diverse syllable types with broad spectral, temporal, and spectrotemporal features. Fundamental frequencies ranged from 1.5 to 35 kHz, overall frequencies from 1 to 95 kHz, and durations from 1 to 100 ms. We also observed diverse spectrotemporal patterns. Syllable bandwidths varied from relatively constant frequencies to up to nine octaves and spectrotemporal shapes included downward, upward, sinusoidal, and broadband (noisy) components. Although we observed a highly diverse repertoire, our study does not report the entire spectrum of vocal diversity in this species since we only used vocalizations if they were unambiguously correlated with recognizable behaviors and observed in multiple individuals.

#### B. Common syllables

One of our major findings was that syllables were not necessarily unique to a particular call, but rather the same syllables were used in different calls or song. One possible benefit of using the same syllables in different calls is that it allows for an expansion of the vocal repertoire without producing new syllables. This is well illustrated by the ubiquitous use of down FM syllables. For example, the down FM syllables in irritation calls were acoustically indistinguishable from those in the buzz phrases of song.

Not only were syllables shared among different social vocalizations, we also found that FM pulses emitted for echolocation were used in social communication, and were even embedded within song (song type A syllables). Recent research has shown that echolocation buzzes emitted while bats are foraging are also nearly indistinguishable from buzzes from songs (Schwartz *et al.*, 2007). The idea that echolocation calls may serve communicative functions is not new (reviewed in Altringham and Fenton, 2003). Echolocation calls have been shown to contain information on identity (Masters *et al.*, 1995), age (Masters *et al.*, 1995), sex (Kazial and Masters, 2004), or social group (Pearl and Fenton, 1996) and in at least one study bats also responded to this information (Kazial and Masters, 2004). Echolocation calls can also be emitted intermittently with social calls or may be modified to become social calls (Fenton, 2003). In *T. brasiliensis*, however, the use of echolocation pulses is different in that they are used while performing courtship displays with no echolocation function and are embedded into highly stereotyped social communication signals.

#### C. Temporal patterns

The most salient differences between some calls were their temporal emission patterns rather than syllable acous-

tics. Clicks are a good example. Although questioning clicks, anticipation clicks, and nose-rubbing calls are emitted in very different behavioral contexts and likely convey different information, they do not differ in the acoustic features of the click syllables themselves. These calls have different syllable distributions: Questioning clicks were emitted randomly, anticipation clicks were emitted singly, and nose-rubbing calls were always emitted in distinctive groups. Interestingly, temporal emission patterns are also important in sperm whales (Weilgart and Whitehead, 1997), one of the only mammals other than bats (Schmidt-French *et al.*, 2006) that use clicks for social communication. Sperm whales emit codas, which are highly stereotyped series of clicks (Rendell and Whitehead, 2005). Codas vary between social groups in both the number of clicks and the pattern of intervals between clicks. Although we use clicks as an example, temporal emissions patterns are also important for differentiating between long calls and between down FM calls.

Calls not only varied in the distribution of temporal emissions (i.e., whether or not syllables were clumped) but also in emission features. For example, the emission rate (calls/s) varied greatly between calls with similar syllable acoustics (e.g., mounting and alarm calls). On the other hand, the most salient difference for some multisyllabic vocalizations, such as calls and phrases composed of low frequency down FM syllables, was the number of syllables per call. Although syllable number may be rather important and stereotyped in some vocalizations, in other calls, such as face-rubbing and nose-rubbing calls, syllable number was more variable. Thus, in these calls, syllable number may not be a reliable feature even if the calls are always produced in a multisyllabic fashion.

#### D. Call composition

We found that multiple components of song were similar to other calls. For example, type A syllables in song were similar to echolocation pulses and trill phrases were similar to herding calls. Thus, both individual elements (syllables) and multiple elements (multisyllabic calls) were embedded into more complex vocalizations. One implication of this finding is that information may be conveyed by the acoustic context of syllables or the way in which they are combined.

Combining calls or notes to form new sequences has been observed in other taxa (Cleveland and Snowdon, 1982; Robinson, 1984; Hailman and Ficken, 1986; Crockford and Boesch, 2005; Arnold and Zuberbühler, 2006a). In some birds and primates, higher order combinations or the presence of particular elements elicit different responses from receivers and thus appear to affect signal meaning (Freeberg and Lucas, 2002; Clucas *et al.*, 2004; Arnold and Zuberbühler, 2006b). Future research on how syllables are combined and perceived may determine whether this is also the case in bats.

#### E. Determining call boundaries

In this study, we used a quantitative analysis of temporal patterns to determine whether calls were mono- or multisyllabic and to determine inter- and intracall boundaries. Most

studies have either not addressed temporal emission patterns or relied on a qualitative approach for determining call (or bout) boundaries over time. For example in bats, bouts of vocalizations (termed “calls,” “syllable trains,” or “phrases”) have been identified as sequences of syllables where the interval between syllables is less than the duration of the preceding syllable, less than the duration of the two syllables surrounding the interval, or less than the mean length of the two neighboring syllables (Kanwal *et al.*, 1994; Behr and von Helversen, 2004; Ma *et al.*, 2006). These methods are inconsistent between studies and impossible to implement across vocalizations with a broad range of durations (in this study, 1–100 ms) or intervals between syllables (in this study, 3–100 ms). Furthermore, since these thresholds are set by the researchers, they often do not reflect salient features of the vocalizations themselves. For example, using one of the criteria mentioned above, maternal directives would be considered monosyllabic (average duration = 21 ms, Table III; average intersyllable interval within calls = 60 ms, Table II) even though these vocalizations are always produced in distinct groups (Fig. 1).

An important aspect of our examination of temporal emission patterns is that they provide working hypotheses for vocal perception. Our results suggest that the meaning conveyed by calls may also be determined in part by the temporal emissions of syllables. In primates, research has shown that for some vocalizations, multiple syllables are the units of perception (Hauser *et al.*, 1998; Ghazanfar *et al.*, 2001) rather than single syllables. In *T. brasiliensis*, we hypothesize that for multisyllabic calls that are always emitted in groups and never alone, the groups of syllables are likely the units of perception rather than individual syllables. Perceptual research has also indicated that temporal emission features, such as the number of syllables per call and the interval between syllables, are important for call perception in primates (Hauser *et al.*, 1998; Ghazanfar *et al.*, 2002) and may also be the case in bats.

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