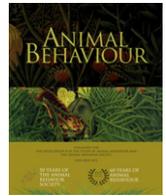


Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Social context evokes rapid changes in bat song syntax

Kirsten M. Bohn*, Grace C. Smarsh, Michael Smotherman

Department of Biology, Texas A&M University, College Station, TX, U.S.A.

ARTICLE INFO

Article history:

Received 11 December 2012
 Initial acceptance 7 January 2013
 Final acceptance 29 March 2013
 Available online xxx
 MS. number: A12-00940R

Keywords:

bat
 echolocation
 song
 syntax
Tadarida brasiliensis

The capacity to modify vocal syntax to changes in social context is an important component of vocal plasticity and complexity in adult vertebrates, especially in human speech. The ecological significance of this behaviour has been well established in some avian species but not in mammals where complex, multisyllabic vocalizations are rare. The Brazilian free-tailed bat, *Tadarida brasiliensis*, is a mammal that sings like a bird, producing hierarchically structured songs that vary in the order and number of phrases (i.e. syntax) from one rendition to the next while simultaneously following specific organizational rules. Here, we used playback experiments to examine the function of songs and tested whether song syntax is correlated with social context. Free-tailed bats responded rapidly and robustly to echolocation calls that mimicked a bat flying past the roost but did not respond to conspecific song playbacks. We compared songs that were directed at a passing bat with songs that were produced spontaneously and found that bats produced longer songs with different phrase content and order when singing spontaneously than when singing to bats approaching their roost. Thus, free-tailed bats quickly varied song composition to meet the specific demands of different social functions. These distinct singing behaviours are similar to those of some songbirds, suggesting that bats and birds have converged upon a similar set of production modes that may reflect common neural mechanisms and ecological factors.

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

An important milestone in the evolution of animal communication is the transition from monosyllabic to polysyllabic vocalizations (Maynard Smith & Szathmáry 1995). While the information in monosyllabic vocalizations is limited to changes in the acoustic features of a syllable (phonology), multiple syllables add an entirely new dimension of potential flexibility and information, namely syntax, or the way in which elements are ordered and combined. The use of learned, multisyllabic vocalizations with flexible syntax is most widely seen in birds (Kroodsma & Miller 1996). Songbirds are especially well known for the widespread use of multisyllabic songs associated with mating and territorial defence (Marler & Slabbekoorn 2004; Catchpole & Slater 2008). Syntax in birdsong is salient (Balaban 1988), and social context may play a large role in song structure and note use (Catchpole & Slater 2008; Byers & Kroodsma 2009).

In contrast, most mammals produce monosyllabic, fixed signals with much less flexibility than birds (Hammerschmidt & Fischer 2008; Snowdon 2009; but see Arnold & Zuberbühler 2006; Clarke et al. 2006; Ouattara et al. 2009). Although various examples of singing have been documented in mammals (Payne & McVay 1971; Mitani & Marler 1989; Davidson & Wilkinson 2002; Behr &

von Helversen 2004; Holy & Guo 2005; Clarke et al. 2006; Bohn et al. 2009), there is no evidence that mammals alter song composition and structure in ways comparable to songbirds. This key behavioural distinction has been attributed to the general absence of a neural substrate supporting vocal plasticity in mammals that is present in both songbirds and humans (Doupe & Kuhl 1999; Jarvis et al. 2005; Kao et al. 2005; Jürgens 2009).

Cetaceans and bats may be exceptional since both groups have evolved a suite of neural adaptations to support laryngeal echolocation. They are the only two groups of mammals that demonstrate vocal learning (Boughman 1998; Janik 2000; Foote et al. 2006; Knörnschild et al. 2010), juvenile babbling (Knörnschild et al. 2006), regional dialects (Cerchio et al. 2001; Ouattara et al. 2009) and cultural transmission of vocalizations (Deecke et al. 2000; Garland et al. 2011). If these behaviours are indicative of a neural substrate that supports vocal plasticity, it is likely that some cetaceans and bats may also possess the capacity to rapidly vary vocal syntax in response to social cues.

Brazilian free-tailed bats, *Tadarida brasiliensis*, produce songs that are remarkably similar acoustically and behaviourally to birdsongs. Free-tailed bat songs follow a hierarchical structure where three types of phrases (chirps, trills and buzzes) are in turn composed of four types of syllables (Chirp A, Chirp B, trill and buzz; Bohn et al. 2009; Fig. 1). Free-tailed bat songs are highly flexible while following a clear and consistent syntax. The number and order of phrases dynamically vary from one rendition to the next, while

* Correspondence and present address: K. M. Bohn, School of Integrated Science and Humanity, Florida International University, Miami, FL 33199, U.S.A.
 E-mail address: kbohn@fiu.edu (K. M. Bohn).

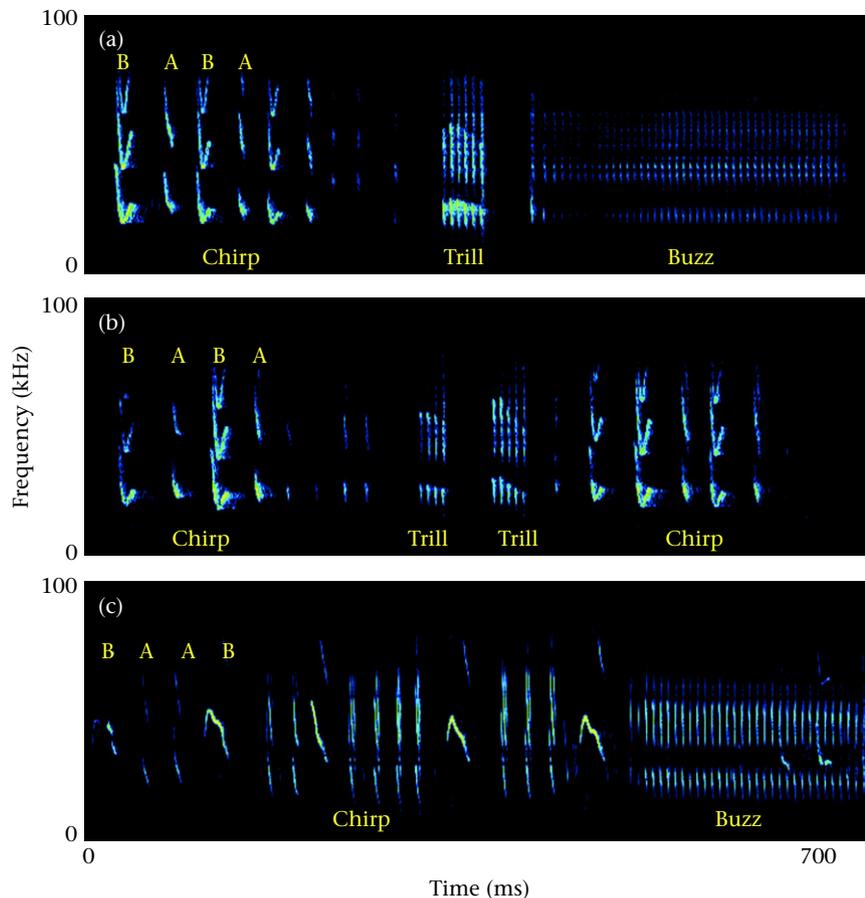


Figure 1. Spectrograms of songs produced by male free-tailed bats. (a) A bat produces a chirp-trill-buzz song type in response to an echolocation playback (Supplementary Audio S1). (b) The same bat produces a chirp-trill-chirp song type spontaneously in the roost (Supplementary Audio S2). (c) A different bat produces a chirp-buzz song type (Supplementary Audio S3). Upper case letters refer to the first four Chirp A and Chirp B syllables. Note that for the song in (b), the complete phrase sequence is chirp-trill-trill-chirp, but when defining 'song types', sequential repetitions of phrases are omitted.

simultaneously adhering to a specific set of rules (Bohn et al. 2009). Although some “song types” are preferred over others (Fig. 1), the number of repeats of trill and buzz phrases vary within each song type. Thus, a few element types (in this case phrases) can be combined to form a potentially enormous set of unique signals. This ‘combinatorial syntax’ (Hailman & Ficken 1986) has been observed in only a handful of avian species including chickadees (Hailman & Ficken 1986; Hailman et al. 1987; Ficken et al. 1994) parrots (Wright & Dahlin 2007) and hummingbirds (Rusch et al. 1996).

As in songbirds, free-tailed bat songs are produced exclusively by males and singing is especially pronounced during the mating season. During this time, males establish territories that they aggressively defend against other males, but in which they allow females to reside (Bohn et al. 2008). However, males also sing year round and in all-male colonies, so songs may function in other social contexts besides mating. This is remarkably similar to chickadee calls, which have combinatorial syntax that varies with social (Ficken et al. 1994) and environmental (Soard & Ritchison 2009) context. Free-tailed bats have a large vocal repertoire (Bohn et al. 2008), roost in the millions and have all-male, all-female or mixed-sex colonies that fluctuate across seasons. Thus, the broad diversity of song types may reflect behavioural responses to a highly variable social environment.

Due to the cryptic nature of bats, as well as the short duration, fast tempo, and ultrasonic frequencies of their songs, it has been difficult to discern specific stimuli or behavioural contexts that evoke singing. Since visual cues are generally unavailable to detect

conspecifics from within roost sites, we hypothesized that bats use auditory stimuli to assess social context and that songs may be primarily used to advertise males’ hidden locations to flying conspecifics. In this study we used playbacks of echolocation passes and conspecific songs to determine whether they evoke singing and to test whether bats vary their songs with social context.

METHODS

Playbacks

We conducted 10 playback experiments, each at a different location at a natural roosting site located on the Texas A&M University campus (College Station, TX, U.S.A.). At this site, bats roost in discrete locations in cracks that run between the concrete slabs of the football stadium. We selected 10 roost sites that were outside of the hearing range of each other and placed two speakers and a microphone within 0.25 m of the crack. Each playback experiment consisted of two types of playbacks, echolocation and song. In addition, we conducted five echolocation playbacks within a vivarium using captive *T. brasiliensis*, where one male singer was present at a time ($N = 5$ males). The Texas A&M Animal Care and Use Committee approved all procedures and animal husbandry for this research (protocol number 2007-254). Stimuli were played from a laptop computer running Avisoft Recorder® through a PCMCIA card (NI DAQCard-6062E) to a Pioneer ribbon tweeter (ART-55D), via a Sony power amplifier (STR-DE598).

To create echolocation stimuli, echolocation passes were recorded from five males, one at a time, that were free flying in a $6 \times 2 \times 3$ m flight-room lined with acoustic foam. The microphone (Bruel & Kjaer, type 4939, $\frac{1}{4}$ inch) was placed in the centre of the room where echolocation passes were recorded as the bats flew over the microphone, resulting in an amplitude pattern that mimicked a wild bat's approach during playbacks (Fig. 2). Although the echolocation passes recorded from captive bats differed somewhat from those of wild bats, they were produced in similar highly cluttered environments (at the wild colony, ca. 2 m of space in front of each roosting site is surrounded by cement). Echolocation passes were digitized with a National Instruments DAQmx card, NI PCI-6251 (300 kHz, 16-bit sample rate) and Avisoft software (v.2.97, Avisoft Bioacoustics, Berlin). Song stimuli were obtained from previous recordings we had performed in captive colonies where songs were produced spontaneously in the roosts (Bohn et al. 2009; Fig. 2). Three songs with high signal-to-noise ratios were selected from each of five males. For echolocation passes and songs, intervals between syllables were replaced by silence, and a small (0.5 ms) taper was added to the beginning and end of each syllable using Signal 4.0 (Engineering Design, Belmont, MA, U.S.A.). Files were then band-pass filtered between

5 kHz and 80 kHz and peak-to-peak amplitudes were normalized to 1.5 V.

One bout of three echolocation passes and one bout of three songs were created for each caller ($N = 5$ for echolocation, $N = 5$ for song) using random intervals from recordings (between 3.5 and 9.5 s for echolocation and between 0.3 and 5 s for song; Fig. 2). Each echolocation playback and each song playback consisted of alternating 270 s of background noise with one bout from each of the five callers in random order. Echolocation bout durations ranged from 15 to 19 s, while song bout durations ranged from 6 to 13 s. The different durations for echolocation and song stimuli resulted in each echolocation playback lasting about 24 min and each song playback lasting about 21 min. For all analyses we corrected for this by examining the number of responses per second. In the laboratory, only echolocation playbacks were conducted. In the field, the entire echolocation playback and the entire song playback were conducted in alternating order at each site.

Responses

Vocalizations were recorded and digitized using an Avisoft CM16 condenser microphone and Avisoft Ultrasoundgate[®]

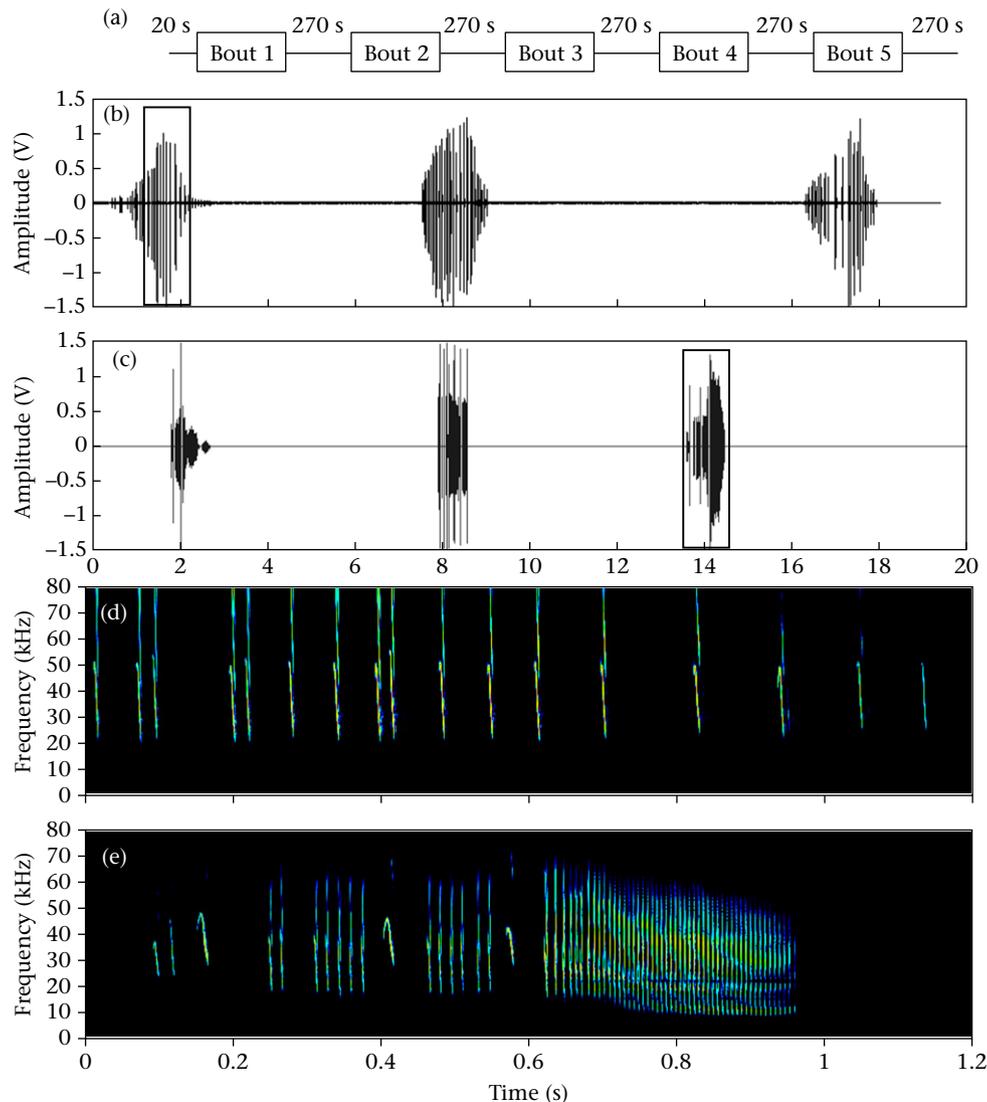


Figure 2. Examples of playbacks. (a) Diagram of an entire playback of echolocation passes or songs. Each bout is from a different individual. (b) A bout of echolocation passes from one bat. (c) A bout of songs from one bat. (d) Spectrograms of the boxed portion of (a). (e) Spectrogram of the boxed portion of (b).

(300 kHz/16 bit). Recordings were divided into four contiguous periods: (1) 20 s pre, immediately preceding stimuli, (2) echo or song, beginning with and encompassing stimuli, (3) 20 s post, immediately following stimuli and (4) 230 s control. For responses, songs were identified from other vocalizations by their unique alternating temporal pattern of Chirp A and Chirp B syllables (Fig. 1; also see Bohn et al. 2009). We visually inspected all recordings and noted the duration and phrase sequence (each chirp, trill and buzz phrase) of every song. Additionally, because sequences were so variable, we also categorized songs into 'song types' by excluding repeats of trills and buzz phrases (Fig. 1).

Analyses

We examined the number of song responses in two ways. First, we pooled responses across all experiments for each stimulus type and for each playback caller ($N = 5$ bats' echolocation passes, $N = 5$ bats' songs) and used a randomized block design ANOVA with playback caller as a block, and period (control, pre, echo/song, post) and stimulus type (echo or song) as factors. To verify whether our findings were consistent across experiments and not due to one exaggerated experiment, we performed an ANOVA as above, but instead of pooling all responses, we kept each experiment separate as a block ($N = 10$ sites in the wild). Statistics were conducted identically for the captive colony experiments except they lacked the song/echo effect (only echo playbacks were performed) and there were only five experiments, each on a separate subject.

Using the experiments conducted at the natural colony, we compared song structure during two distinct contexts: songs produced during an echolocation pass (see Results, Fig. 3) and songs produced spontaneously in the roost during control and pre periods of all playbacks. For this analysis, we did not use post periods because song production was slightly elevated and may have been in response to stimuli. We also did not use responses to song stimuli because there were almost no songs produced during these periods. Although we were unaware what specifically triggered spontaneous songs, we knew it was not a passing bat since no bats were flying during these experiments.

First, we used a chi-square contingency test to compare the frequency of the four most common song types (phrase order with buzz and trill repeats ignored) and complete phrase sequences (including repeats) between echolocation playback periods (echo) and control/pre periods (spontaneous). To test whether individuals modified songs between contexts, we identified individuals using their Chirp B syllables, which are highly stereotyped within

individuals but vary among individuals (Bohn et al. 2008). We identified eight bats for which we had at least 10 songs and performed a logistic regression using context as a factor and subject as a block on the same song type and phrase order categories as the chi-square contingency test. In addition, we identified 21 bats for which we had at least five songs in both contexts and used paired t tests to compare the duration of songs, the frequency of songs with buzzes and the frequency of songs with trills between the two contexts. Finally, for bats that produced trills or buzzes in at least five songs in both contexts ($N = 15$ and 18, respectively), we used t tests to determine whether the number of repeats varied between contexts.

RESULTS

During 10 playback experiments, we recorded songs at a rate of more than 100 songs/h, with a total of 699 songs from 39 different males (equipment failed during one song playback). Although the number of singing males varied between roost sites, the density of singers at a given site did not affect individual singing rates (regression of average number of songs per male versus number of males in a site: $F_{1,9} = 0.14$, $P = 0.7$). Bats responded to echolocation passes but not to conspecific songs (ANOVA: song/echo: $F_{1,31} = 20.6$, $P < 0.0001$; control/pre/stimulus/post: $F_{3,31} = 29.0$, $P < 0.0001$; interaction: $F_{3,31} = 24.8$, $P < 0.0001$; Figs 3, 4a). The only significant difference following Tukey tests ($\alpha = 0.05$) was between echolocation periods and all others. These effects were robust in that the same results were found when data were analysed relative to each experiment (song/echo: $F_{1,359} = 25.8$, $P < 0.0001$; control/pre/stimulus/post: $F_{3,359} = 36.3$, $P < 0.0001$; interaction: $F_{3,359} = 31.0$, $P < 0.0001$).

Responses to echolocation passes were both rapid and robust. Out of 50 sets of echolocation passes ($N = 5$ different bats' passes per playback, $N = 10$ playbacks), bats responded 74% of the time with a total of 215 songs. During the interval immediately preceding stimuli, we recorded songs only 6% of the time across all experiments (three songs). Echolocation-provoked singing occurred very rapidly with onset latencies ranging from 200 to 500 ms (Fig. 3). We also ran echolocation playbacks on isolated males in our captive colony and found similar results: singing was rapidly and robustly provoked via playbacks of echolocation passes ($F_{3,12} = 16.05$, $P = 0.0002$; mean \pm SE number of songs/20 s: echo stimulus = 5.8 ± 1.2 ; pre = 0.13 ± 0.08 ; post = 0.93 ± 0.46 ; control = 0.14 ± 0.07 ; analysed relative to subject: $F_{3,54} = 15.6$, $P < 0.0001$; Fig. 3; Supplementary Video S1, Audio S4).

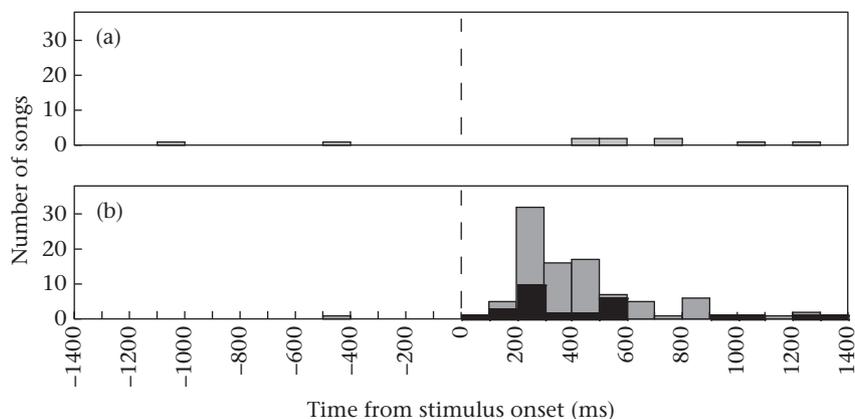


Figure 3. Number of songs produced by bats at 100 ms intervals relative to the start of stimulus onset of (a) songs ($N = 135$ stimulus songs, $N = 10$ response songs) or (b) echolocation passes ($N = 135$ stimulus echolocation passes, $N = 92$ response songs). In (b), grey bars represent wild bats' responses; black bars are superimposed and represent captive bats' responses ($N = 28$ songs, $N = 45$ echolocation passes).

For the natural colony experiments, we tested whether the composition of songs produced during the stimulus periods of echolocation playbacks differed from those produced spontaneously in the roost. First, we examined the distribution of phrase sequences and song types. There were a total of 69 different phrase sequences, of which 52% were the four most common sequences: chirp, chirp-buzz, chirp-trill-buzz and chirp-trill-trill-buzz). We found no correlation between phrase sequences and context using the four most common sequences and pooling the remainder into an 'other' category ($\chi^2_4 = 7.0$, $N = 587$ songs, $P = 0.14$). There was also no difference between contexts for eight bats that produced at least 10 songs in each context (logistic regression: $\chi^2_4 = 4.2$, $P = 0.28$). There were 26 song types (phrase sequences excluding trill and buzz repetitions (Fig. 1, Table 1), of which 84% were the four most common types: chirp-trill-buzz, chirp-buzz, chirp-trill and chirp. Comparing the relative frequency of these song types and a fifth 'other' category between echolocation and spontaneous contexts revealed that more songs during echolocation passes were chirp-trill-buzz than expected (38% of 213 echolocation response songs versus 28% of 385 spontaneous songs), whereas more spontaneous songs were chirp-trill (13% versus 7%) or chirp (22% versus 15%) than expected ($\chi^2_4 = 13.0$, $P = 0.01$). There was no significant difference in the frequency of chirp-buzz song types (24% and 21% for echo and spontaneous, respectively) or in the frequency of 'other' songs (16% in both contexts). We used a logistic regression on the same song types with bat as a block and context as a factor for eight bats that had at least 10 songs in each context and found similar results ($\chi^2_4 = 22.0$, $P = 0.0002$; mean percentage of song types during echo and spontaneous contexts: chirp: 16% and 26%; chirp-trill: 3% and 18%; chirp-buzz: 27% and 15%; chirp-trill-buzz: 40% and 27%; other: 18% and 13%).

Next, we examined four song parameters for individuals that produced at least five songs in the two contexts: duration, number of phrases, whether or not songs contained buzzes and whether or not songs contained trills. We found that songs produced during echolocation stimuli were significantly shorter but also more frequently included buzz phrases than spontaneously produced songs (paired t tests: duration: $t_{20} = 2.8$, $P = 0.01$, Fig. 4b; buzz phrase: $t_{20} = 2.7$, $P = 0.01$, Fig. 4c). There was no difference between songs produced in the two contexts with respect to the frequency of trills ($t_{20} = 0.64$, $P = 0.53$) or number of phrases ($t_{20} = 0.20$, $P = 0.84$). Finally, we tested whether the number of phrase repeats differed between contexts for those songs that contained buzzes or trills. We found no difference between contexts for the number of buzz repeats ($t_{17} = 0.81$, $P = 0.43$) or trill repeats ($t_{14} = 1.7$, $P = 0.10$).

DISCUSSION

Playbacks mimicking the echolocation call sequences of passing bats rapidly triggered stimulus-specific singing. The rapid response

Table 1

Distribution of song types produced by Brazilian free-tailed bats at the wild colony during playback experiments

Song type	N songs	Percentage
chirp-trill-buzz	243	34.8
chirp-buzz	148	21.2
chirp	134	19.2
chirp-trill	65	9.3
chirp-trill-chirp	27	3.9
chirp-trill-chirp-buzz	27	3.9
chirp-trill-chirp-trill-buzz	17	2.4
chirp-trill-chirp-trill	5	0.7
Other ($N=18$ song types)	33	4.7
26 song types	699	

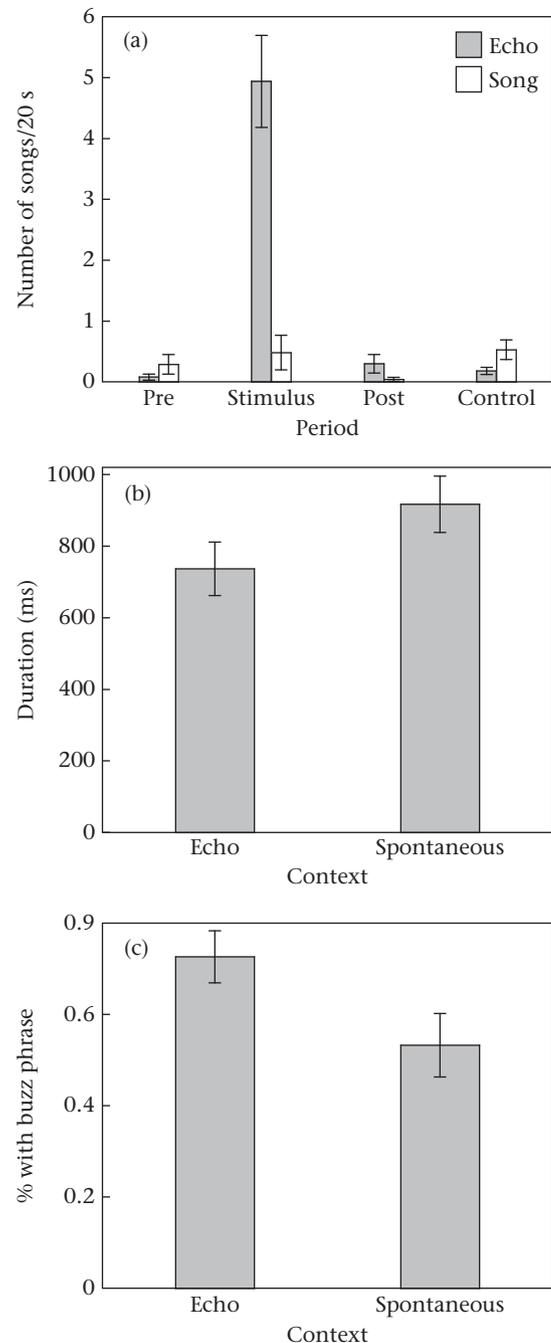


Figure 4. (a) Songs produced by bats before (pre), during (stimulus) and after (post) playback of echolocation and song stimuli, and during the control period (control). (b) Song duration and (c) percentage of songs with buzzes produced in response to echolocation stimuli and produced spontaneously (control and pre periods of (a)).

and tight temporal correlation between the echolocation pulse stimuli and the onset of the bats' singing leaves little doubt that the evoked songs were directed to the perceived presence of a passing bat. Although our experiments were conducted during the day, when few bats normally fly (except between roosts), we obtained the same results in the laboratory and when bats were actually flying (Video S1). Thus, we are confident that bat song is a robust and natural response to approaching conspecifics. Conspecific song, however, did not evoke singing, even though the spectrotemporal acoustic structure of some song syllables are very similar to

echolocation pulses (Bohn et al. 2008). This indicates that the overlying temporal pattern of acoustic stimuli influenced the bats' responses.

The rapid responses of bats to the echolocation pulses of approaching conspecifics exemplify the use of echolocation signals for social interactions. By eavesdropping on echolocation signals, males can sing when they are certain a conspecific is in audible range. Interestingly, echolocation calls of approaching conspecifics also trigger song in the greater sac-winged bat, *Saccopteryx bilineata* (Knörnschild et al. 2012). In this species, different songs are used based on the gender of the approaching conspecific, indicating that males can identify gender based on echolocation call acoustics (Knörnschild et al. 2012). Although we only played male echolocation calls, it is unlikely that free-tailed bats recognize the gender of the caller since research has shown that there is a great deal of within-individual variation in echolocation calls in this species and no differences between males and females in echolocation call structure (Gillam & McCracken 2007).

Echolocation-evoked songs were more likely to include all three of the main song phrases but were shorter than spontaneous songs. The shorter duration of these songs was not attributable to fewer numbers of phrases but instead likely reflect shorter durations of the phrases themselves. Echolocation-evoked singing likely notifies passing bats of the presence and location of an occupied and suitable day roost, a critical need for migratory bats that may not be familiar with the local territory. These shorter songs are tailored to the context in which they are used because they must rapidly convey sufficient information to capture the attention of a flying conspecific that would pass beyond hearing range within 1–2 s. Although these data do not show whether echo-induced songs are directed exclusively at females or males, these songs may serve both functions; attracting females and warning males, much like what is seen in songbirds (Kroodsma & Miller 1996). The function of spontaneous singing is less clear. Song variation may reflect a variety of social contexts in these densely crowded roosts, such as attracting females to the male's location within the roost, defining or maintaining dominance hierarchies, or promoting group cohesion.

Our finding that free-tailed bats vary the syntax of their songs in different social contexts is unique among mammals. Chick-a-dee calls that have similar combinatorial syntax also show correlations between sequence order and social context (Ficken et al. 1994). However, even songbirds that do not use combinatorial syntax, per se, and can vary song structure and syntax across different contexts (Sossinka & Böhner 1980; Dunn & Zann 1996; Woolley & Doupe 2008; Byers & Kroodsma 2009). This variability has been closely tied to neural activity in an avian analogue of the mammalian striothalamocortical network, the songbirds' anterior forebrain pathway (Jarvis et al. 1998, 2005; Kao et al. 2005). A similar network is believed to be important for speech (Jarvis 2004), and, in a pathological state, may underlie a plethora of human speech disorders (Lieberman 2007). Striatal dopamine subserves vertebrate vocal plasticity and appears to be a key substance for inducing song variability (Jarvis et al. 1998; Kao et al. 2005). In mammals, incorporation of the striothalamic network into the vocal control circuitry may have been a critical step towards the evolution of human speech (Doupe & Kuhl 1999; Jarvis 2004; Jürgens 2009), yet vocal plasticity is rare in mammals with correspondingly little evidence that the basal ganglia participates in mammalian vocal communication (Jürgens 2009). Unlike most mammals, however, echolocating bats routinely modulate the timing and acoustic structure of their vocalizations. Free-tailed bats show vocalization-related neuronal activity in the dorsolateral striatum (Schwartz & Smotherman 2011) and pharmacological manipulations of striatal dopamine profoundly influence

sensorimotor control of the free-tailed bat's voice (Tressler et al. 2011). We have yet to show whether bat song composition is directly influenced by basal ganglia activity, but similarities in the way free-tailed bats and songbirds vary song composition indicate the two disparate groups may share common design elements within their song control circuitry. Identifying the neural basis for these similarities may provide a useful new avenue for exploring how, when and why vocal plasticity evolved in mammals.

Acknowledgments

We thank our undergraduate research assistants N. Tedford, S. Trent, K. Rogers and M. Gutierrez for help conducting experiments and collecting data at the field sites. We thank B. Earnest and J. Jarvis for help training bats and maintaining the captive colony, and P. Narins and W. Metzner for comments on an earlier version of the manuscript. We are particularly grateful to the Texas A&M Department of Athletics for providing access to the bats and allowing us to conduct these experiments within and around their facilities. This research was supported by Texas A&M University.

Supplementary Material

Supplementary material for this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.04.002>.

References

- Arnold, K. & Zuberbühler, K. 2006. Semantic combinations in primate calls. *Nature*, **441**, 303.
- Balaban, E. 1988. Bird song syntax: learned intraspecific variation is meaningful. *Proceedings of the National Academy of Sciences, U.S.A.*, **85**, 3657–3660.
- Behr, O. & von Helversen, O. 2004. Bat serenades: complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behavioral Ecology and Sociobiology*, **56**, 106–115.
- Bohn, K. M., Schmidt-French, B., Ma, S. T. & Pollak, G. D. 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.
- Bohn, K. M., Schmidt-French, B., Schwartz, C., Smotherman, M. & Pollak, G. 2009. Versatility and stereotypy of free-tailed bat songs. *PLoS One*, **4**, e6746.
- Boughman, J. W. 1998. Vocal learning by greater spear-nosed bats. *Proceedings of the Royal Society B*, **265**, 227–233.
- Byers, B. E. & Kroodsma, D. E. 2009. Female mate choice and songbird song repertoires. *Animal Behaviour*, **77**, 13–22.
- Catchpole, C. K. & Slater, P. J. B. 2008. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Cerchio, S., Jacobsen, J. K. & Norris, T. F. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Animal Behaviour*, **62**, 313–329.
- Clarke, E., Reichard, U. H. & Zuberbühler, K. 2006. The syntax and meaning of wild gibbon songs. *PLoS One*, **1**, e73.
- Davidson, S. M. & Wilkinson, G. S. 2002. Geographic and individual variation in vocalizations by male *Saccopteryx bilineata* (Chiroptera: Emballonuridae). *Journal of Mammalogy*, **83**, 526–535.
- Deecke, V. B., Ford, J. K. B. & Spong, P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour*, **60**, 629–638.
- Doupe, A. J. & Kuhl, P. K. 1999. Birdsong and human speech: common themes and mechanisms. *Annual Review of Neuroscience*, **22**, 567–631.
- Dunn, A. M. & Zann, D. A. 1996. Undirected song in wild zebra finch flocks: contexts and effects of mate removal. *Ethology*, **102**, 529–539.
- Ficken, M. S., Hailman, E. D. & Hailman, J. P. 1994. The chick-a-dee call system of the Mexican chickadee. *Condor*, **96**, 70–82.
- Footo, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O. & Hoelzel, A. R. 2006. Killer whales are capable of vocal learning. *Biology Letters*, **2**, 509–512.
- Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., Poole, M. M., Robbins, J. & Noad, M. J. 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, **21**, 687–691.
- Gillam, E. H. & McCracken, G. F. 2007. Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment. *Animal Behaviour*, **74**, 277–286.
- Hailman, J. P. & Ficken, M. S. 1986. Combinatorial animal communication with computable syntax: chick-a-dee calling qualifies as 'language' by structural linguistics. *Animal Behaviour*, **34**, 1899–1901.

- Hailman, J. P., Ficken, M. S. & Ficken, R. W.** 1987. Constraints on the structure of combinatorial 'chick-a-dee' calls. *Ethology*, **75**, 62–80.
- Hammerschmidt, K. & Fischer, J.** 2008. Constraints in primate vocal production. In: *Evolution of Communicative Flexibility: Complexity, Creativity, and Adaptability in Human and Animal Communication* (Ed. by D. K. Oller & U. Griebel), pp. 93–119. Cambridge, Massachusetts: MIT Press.
- Holy, T. E. & Guo, Z.** 2005. Ultrasonic songs of male mice. *PLoS Biology*, **3**, e386.
- Janik, V. M.** 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science*, **289**, 1355–1357.
- Jarvis, E. D.** 2004. Learned birdsong and the neurobiology of human language. *Behavioral Neurobiology of Birdsong*, **1016**, 749–777.
- Jarvis, E. D., Scharff, C., Grossman, M. R., Ramos, J. A. & Nottebohm, F.** 1998. For whom the bird sings: context-dependent gene expression. *Neuron*, **21**, 775–788.
- Jarvis, E. D., Gunturkun, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D. J., Shimizu, T., et al.** 2005. Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*, **6**, 151–159.
- Jürgens, U.** 2009. The neural control of vocalizations in mammals: a review. *Journal of Voice*, **23**, 1–10.
- Kao, M. H., Doupe, A. J. & Brainard, M. S.** 2005. Contributions of an avian basal ganglia–forebrain circuit to real-time modulation of song. *Nature*, **433**, 638–643.
- Knörnschild, M., Behr, O. & Von Helversen, O.** 2006. Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*). *Naturwissenschaften*, **93**, 451–454.
- Knörnschild, M., Jung, K., Nagy, M., Metz, M. & Kalko, E.** 2012. Bat echolocation calls facilitate social communication. *Proceedings of the Royal Society B*, **279**, 4827.
- Knörnschild, M., Nagy, M., Metz, M., Mayer, F. & von Helversen, O.** 2010. Complex vocal imitation during ontogeny in a bat. *Biology Letters*, **6**, 156–159.
- Kroodsma, D. E. & Miller, E. H.** 1996. *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca, New York: Comstock.
- Lieberman, P.** 2007. The evolution of human speech. *Current Anthropology*, **48**, 39–66.
- Maynard Smith, J. & Szathmáry, E.** 1995. *The Major Transitions in Evolution*. Oxford: Oxford University Press.
- Marler, P. & Slabbekoorn, H.** 2004. *Nature's Music, the Science of Birdsong*. Amsterdam: Elsevier Academic Press.
- Mitani, J. C. & Marler, P.** 1989. A phonological analysis of male gibbon singing behavior. *Behaviour*, **109**, 20–45.
- Ouattara, K., Lemasson, A. & Zuberbühler, K.** 2009. Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences, U.S.A.*, **106**, 22026–22031.
- Payne, R. S. & McVay, S.** 1971. Songs of humpback whales. *Science*, **173**, 585–597.
- Rusch, K. M., Pytte, C. L. & Ficken, M. S.** 1996. Organization of agonistic vocalizations in black-chinned hummingbirds. *Condor*, **98**, 557–566.
- Schwartz, C. & Smotherman, M.** 2011. Mapping vocalization-related immediate early gene expression in echolocating bats. *Behavioral Brain Research*, **224**, 358–368.
- Snowdon, C. T.** 2009. Plasticity of communication in nonhuman primates. *Advances in the Study of Behavior*, **40** (40), 239–276.
- Soard, C. M. & Ritchison, G.** 2009. 'Chick-a-dee' calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Animal Behaviour*, **78**, 1447–1453.
- Sossinka, R. & Böhner, J.** 1980. Song types in the zebra finch *Poephila guttata castanotis*. *Zeitschrift für Tierpsychologie*, **53**, 123132.
- Tressler, J., Schwartz, C., Wellman, P., Hughes, S. & Smotherman, M.** 2011. Regulation of bat echolocation pulse acoustics by striatal dopamine. *Journal of Experimental Biology*, **214**, 3238–3247.
- Woolley, S. C. & Doupe, A. J.** 2008. Social context-induced song variation affects female behavior and gene expression. *PLoS Biology*, **6**, e62.
- Wright, T. F. & Dahlin, C. R.** 2007. Pair duets in the yellow-naped amazon (*Amazona auropalliata*): phonology and syntax. *Behaviour*, **144**, 207–228.