



## Social context evokes rapid changes in bat song syntax



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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.

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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).

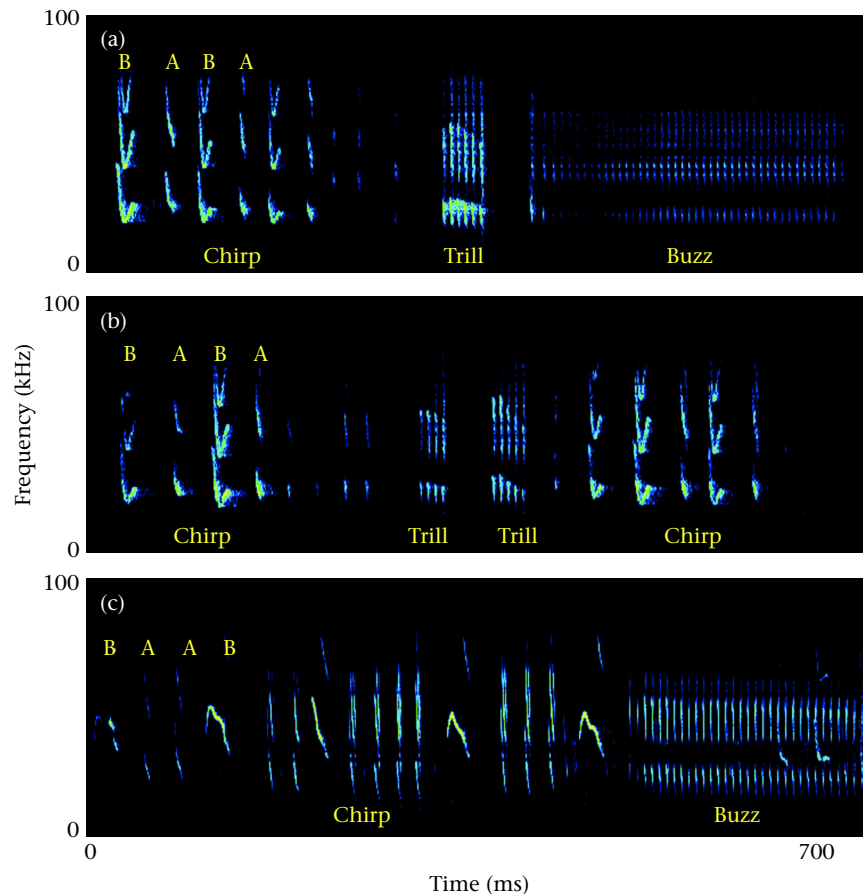
In contrast, most mammals produce monosyllabic, fixed signals with much less flexibility than birds (Hammerschmidt & Fischer 2008; Snowdon 2009; but see Arnold & Zuberbühler 2006; Clarke et al. 2006; Ouattara et al. 2009). Although various examples of singing have been documented in mammals (Payne &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

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**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).

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