



A fine-scale, broadly applicable index of vocal performance: frequency excursion



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ARTICLE INFO

Article history:

Received 15 August 2015

Initial acceptance 22 September 2015

Final acceptance 25 February 2016

MS. number: A15-00707R2

Keywords:

birdsong
chipping sparrow
frequency excursion
song sparrow
swamp sparrow
vocal deviation
vocal performance
vocalization

Our understanding of the evolution and function of animal displays has been advanced through studies of vocal performance. A widely used metric of vocal performance, vocal deviation, is limited by being applicable only to vocal trills, and also overlooks certain fine-scale aspects of song structure that might reflect vocal performance. In light of these limitations we here introduce a new index of vocal performance, 'frequency excursion'. Frequency excursion calculates, for any given song or song segment, the sum of frequency modulations both within and between notes on a per-time basis. We calculated and compared the two performance metrics in three species: chipping sparrows, *Spizella passerina*, swamp sparrows, *Melospiza georgiana*, and song sparrows, *Melospiza melodia*. The two metrics correlated as expected, yet frequency excursion accounted for subtle variations in performance overlooked by vocal deviation. In swamp sparrows, frequency excursion values varied significantly by song type but not by individual. Moreover, song type performance in swamp sparrows, according to both metrics, varied negatively with the extent to which song types were shared among neighbours. In song sparrows, frequency excursion values of trilled song segments exceeded those of nontrilled song segments, although not to a statistically significant degree. We suggest that application of frequency excursion in birds and other taxa will provide new insights into diverse open questions concerning vocal performance, function and evolution.

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Much research in the fields of sexual selection and animal communication has focused on mating signals and displays, produced by animals as they compete for access to prospective mates (Andersson, 1994; Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005; Seyfarth et al., 2010). Some mating displays seem to require high vigour or skill to be performed effectively (Byers, Hebets, & Podos, 2010; Darwin, 1871). As such, only the 'best' signallers in a population should be able to execute the most complex or challenging displays, rendering these displays reliable as indicators of signaller quality (Byers et al., 2010; Cardoso, 2013a). Empirical evidence available to date, while limited, suggests that

variation in display performance can indeed hold functional value, both to males assessing potential competitors and to females assessing prospective mates (e.g. Arak, 1983; Barske, Schlinger, Wikelski, & Fusani, 2011; Reichert & Gerhardt, 2012; Vehrencamp, Bradbury, & Gibson, 1989; Welch, Semlitsch, & Gerhardt, 1998; Wilgers & Hebets, 2011; Zanollo, Griggio, Robertson, & Kleindorfer, 2013).

Useful recent insights into display performance variation and its functional consequences have emerged through studies of vocal displays in vertebrates, including song in songbirds (e.g. Byers, 2007; Nowicki, Peters, & Podos, 1998; Podos, Lahti, & Moseley, 2009; Sakata & Vehrencamp, 2012; Spencer & MacDougall-Shackleton, 2011). Songbirds sing using multiple motor systems, namely the syrinx (sound source), respiratory system and vocal tract (reviewed by: Podos et al., 2009; Podos & Nowicki, 2004;

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Riede & Goller, 2014; Suthers, 2004). Performance challenges arise as birds coordinate syrinx modulations with intricately patterned respiratory movements, and as they track changing source frequencies via precise reconfigurations of the vocal tract (Hoese, Podos, Boetticher, & Nowicki, 2000; Podos, Southall, & Rossi-Santos, 2004b; Riede, Suthers, Fletcher, & Blevins, 2006; Suthers, Vallet, & Kreutzer, 2012; Westneat, Long, Hoese, & Nowicki, 1993). Studies of hand-reared songbirds, in which males are trained with challenging song models, have provided direct experimental evidence that aspects of song structure are indeed limited by vocal performance capacities (Podos, 1996; Podos, Peters, & Nowicki, 2004a; Zollinger & Suthers, 2004; see also Lahti, Moseley, & Podos, 2011).

A key component in studies of vocal performance, in birds or otherwise, is the quantitative analysis of vocal structure, as a means for drawing inferences about vocal performance limitations. One focal point for studies of vocal performance has been vocalizations

that feature repeated sequences of notes or syllables (i.e. trills, e.g. Podos, 1997; Thorpe & Lade, 1961; Fig. 1). Trills with rapid rates of syllable repetition (high 'trill rates') and/or that span wide ranges of fundamental frequencies (high 'frequency bandwidth') should be comparatively hard to perform because they require correspondingly rapid and extensive modulations of components of the vocal apparatus (Podos et al., 2009). Moreover, trill rate and frequency bandwidth should relate to each other inversely, because of an expected trade-off at maximal performance between rates and spans of vocal modulations. An initial structural analysis of trilled song sequences of 34 species of emberizid songbirds supported this expectation: songs in a family-wide trill rate by frequency bandwidth plot show a lower-left skewed triangular distribution, with some trills showing fast trill rates or broad frequency bandwidths but not both concurrently (Podos, 1997). Similar triangular distributions have since been reported for diverse taxa including numerous avian and one mammalian species (e.g. Ballentine, Hyman, & Nowicki, 2004; Beebee, 2004; Cardoso, Atwell, Ketterson, & Price, 2007; Cardoso & Hu, 2011; Cramer & Price, 2007; Derryberry et al., 2012; Illes, Hall, & Vehrencamp, 2006; Janicke, Hahn, Ritz, & Peter, 2008; Juola & Searcy, 2011; Liu, Lohr, Olsen, & Greenberg, 2008; Pasch, George, Campbell, & Phelps, 2011; Price & Lanyon, 2004; Sockman, 2009; see also Wilson, Bitton, Podos, & Mennill, 2014).

Analyses of trill rate and frequency bandwidth, and of trade-offs between the two, not only help describe constraints on trill production but have also provided a means to test the functional relevance of trill performance variations. Trill rate and frequency bandwidth are in themselves useful measures of vocal performance. Moreover, as a composite index of performance for any trill, one can plot a trill sequence of interest on a taxon-wide graph of trill rate by frequency bandwidth, and calculate the offset between the trill in question and the putative performance constraint. Operationally this calculation involves the derivation of a trill rate by frequency bandwidth 'upper-bound regression' (Podos, 1997), and calculation of the orthogonal distance between the upper-bound regression and the trill of interest (Ballentine et al., 2004; Podos, 2001). The resulting distance, termed 'vocal deviation', corresponds inversely to presumed vocal performance requirements (i.e. higher vocal deviations are indicative of low-performance songs). Vocal deviation, trill rate and frequency bandwidth have now been calculated in a diverse array of studies, and shown in some cases to correlate with beak dimensions (Ballentine, 2006; Derryberry et al., 2012; Huber & Podos, 2006; Podos, 2001; Sockman, 2009), body mass and age (Ballentine, 2009), the vigour of solicitation displays or the strength of spatial associations by females (Ballentine et al., 2004; Caro, Sewall, Salvante, & Sockman, 2010; see also Draganoiu, Nagle, & Kreutzer, 2002), the strength and direction of song playback responses by territorial males (Cramer & Price, 2007; DuBois, Nowicki, & Searcy, 2011; Illes et al., 2006; Moseley, Lahti, & Podos, 2013; see also Goodwin & Podos, 2014; de Kort, Eldermire, Cramer, & Vehrencamp, 2009) and body condition or reproductive success (Janicke et al., 2008; Juola & Searcy, 2011).

While vocal deviation has been used widely as a composite index of vocal performance, it is limited in two notable ways. First, it fails to account for subtle phonologically based aspects of vocal structure that may affect performance and thus hold signal value. In particular, vocal deviation cannot account for frequency and temporal variations within syllables, beyond calculated differences between minimum and maximum frequencies. These variations include numbers and sequences of notes within syllables, rates and patterns of frequency modulation within notes and relationships between ending and starting frequencies of sequential notes (e.g. see Figure 1 in Podos et al., 2009; see also Geberzahn & Aubin,

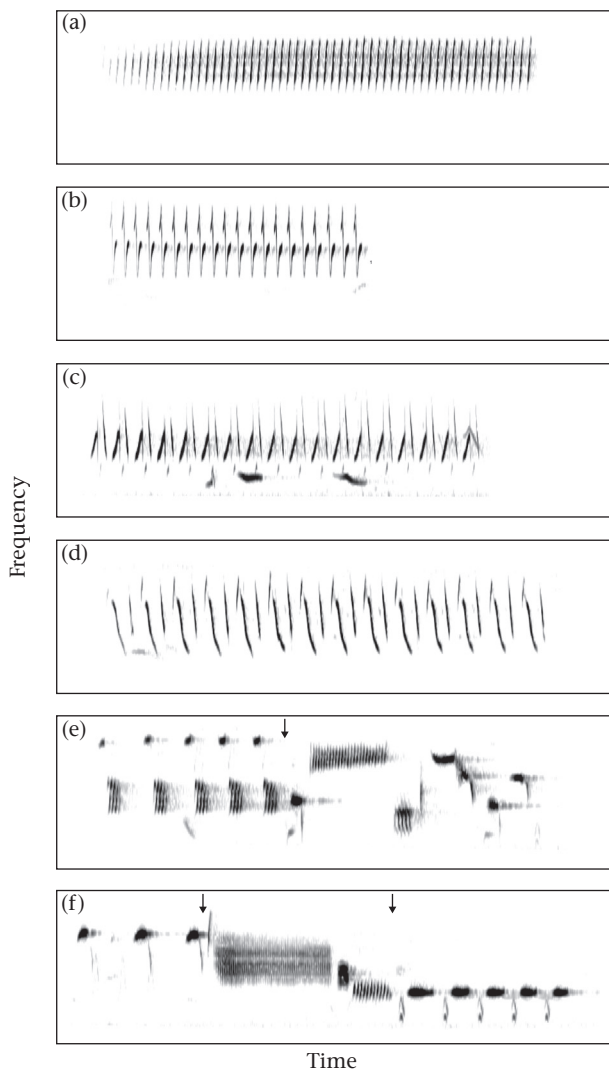


Figure 1. Spectrograms of two songs for each of our three study species. Chipping sparrow songs (a, b) and swamp sparrow songs (c, d) are entirely trilled, whereas song sparrow songs (e, f) feature trilled sequences interspersed with 'note complexes' (groups of notes produced in a nontrilled organization; Marler & Peters, 1987; transitions between trills and note complexes are marked with arrows). Note that the swamp sparrow songs shown here include prominent background noise; syllables with prominent background noise are excluded from performance calculations. Scale: X axis = 0–3 s; Y axis = 0–10 kHz.

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