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

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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,
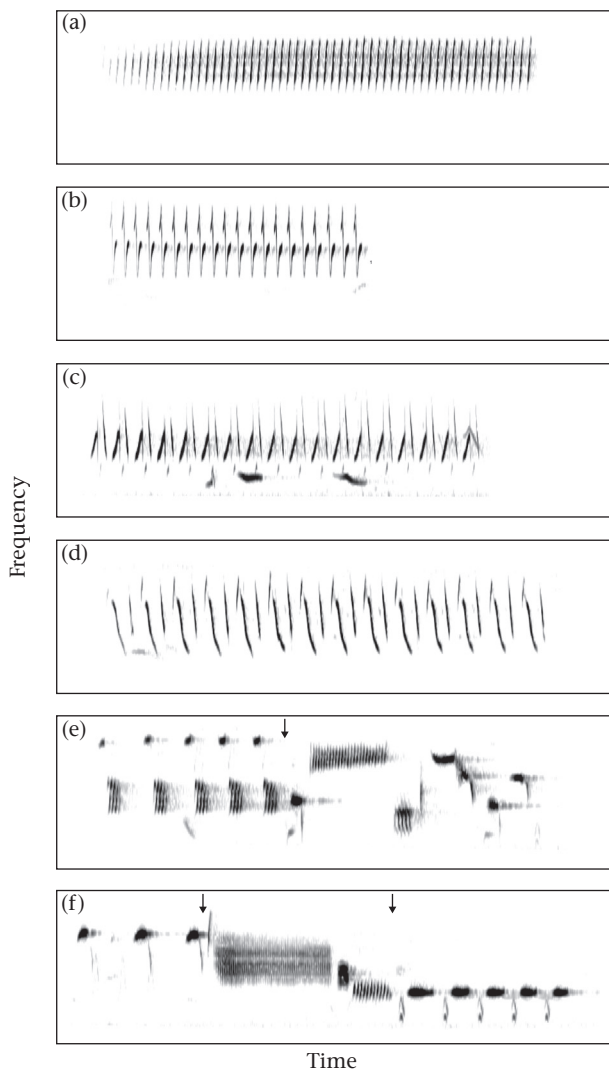
Figure 1. Spectrograms of two songs for each of our three study species. Chipping sparrow songs (a, b) and swamp sparrow songs (c, d) are entirely trilled, whereas song sparrow songs (e, f) feature trilled sequences interspersed with 'note complexes' (groups of notes produced in a nontrilled organization; 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.

2014). In all of these parameters, the production of syllables or syllable sequences with gradually or steadily shifting frequencies should entail less vigorous motor activity than the production of syllables or syllable sequences with rapid or numerous frequency shifts or reversals. A second main limitation of the vocal deviation index is that it can be applied only to trilled sequences (Cardoso, 2014; Geberzahn & Aubin, 2014). While many species trill, others do not, and at present we have no clear guideline for quantifying nontrilled song performances, or for comparing performances of songs with trilled versus nontrilled syntax.

In light of these limitations, we here introduce a new vocal performance index, which we term 'frequency excursion'. The frequency excursion index, which builds upon Taft's (2011, 2014) use of landmarks in spectrogram analysis, aims to account for fine-scale phonological, performance-based variations in song structure and to be applicable irrespective of a vocalization's syntactical organization. Frequency excursion is calculated in two steps, as described in more detail in the Methods section below. First, for each vocal segment of interest, we calculate peak frequencies in successive time bins, thus characterizing the segment's frequency contours. Second, we sum spectrogram 'distances' between successive time by frequency points across the entire sample, including across internote and intersyllable intervals, and standardize this summed distance to a per-second basis. Frequency excursion thus provides a cumulative assessment of frequency modulations that occur across the course of an entire song or song segment. As in Geberzahn and Aubin (2014), frequency excursion accounts for the mechanical performance assumed to occur during silent intervals between notes, following the assumption that reconfigurations of the vocal apparatus are more extensive when note transitions involve larger frequency jumps (see also Cardoso, 2014; Podos et al., 2004b; Westneat et al., 1993). Higher-frequency excursion values should correspond to more active, rapid or extensive vocal activity (i.e. more pronounced reconfigurations of the vocal apparatus per unit time), and thus indicate greater required vocal performance.

Along with this report we are making available a program one of us (J.M.) has written to facilitate the measurement of frequency excursion (see Supplementary Material). We also present sample applications focusing on three diverse questions about vocal performance in three songbird species (Fig. 1): chipping sparrows, *Spizella passerina*, swamp sparrows, *Melospiza georgiana*, and song sparrows, *Melospiza melodia*. First, for all three species we calculated correlations between vocal deviation and frequency excursion to examine how songs' distributions on regression plots corresponded to their spectrographic structure. Following the logic presented above, we expected that frequency excursion would provide a more precise accounting of vocal performance as inferred from spectrograms and based on assumptions about vocal mechanics. We next examined, within our swamp sparrow sample, the following question: for a species with song repertoires and a population that shares song types, how does song performance vary within individuals versus within song types (across individuals)? As first noted by Cardoso, Atwell, Ketterson, and Price (2009, see also 2012), birds with song repertoires likely vary in performance levels across their song types, whereas song types that are shared among birds likely attain similar performance levels across the population. As with dark-eyed juncos, *Junco hyemalis*, we expected that performance variation within the repertoires of individual swamp sparrows would exceed performance variation within shared song types (Cardoso et al., 2009). In our swamp sparrow sample we also compared performance levels of shared versus unshared song types. We predicted that the vocal performance of shared song types would exceed that of unshared song types, following the hypothesis that shared song types provide a means for comparing multiple singers and

thus might be subject to enhanced sexual selection pressures (Logue & Forstmeier, 2008). Consistent with this prediction, Poesel and Nelson (2015) have shown that vocal performance (sensu Forstmeier, Kempenaers, Meyer, & Leisler, 2002) is higher for shared than unshared song types in Puget Sound white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. Finally we examined, within our song sparrow sample, whether performance levels in trilled song sequences exceed those in nontrilled song sequences. This test was possible in song sparrows because their songs include both trilled and nontrilled segments (Fig. 1). Trill structure in numerous species is subject to performance constraints (e.g. Podos, 1996; Suthers et al., 2012; Zollinger & Suthers, 2004), and trills may thus be particularly well suited to reveal variation among males in their performance abilities (e.g. Brumm & Slater, 2006; Cardoso, 2013a; Logue & Forstmeier, 2008; Petruskova et al., 2014; Schmidt, Kunc, Amrhein, & Naguib, 2008). By contrast, limited data are available regarding the performance levels of nontrilled songs. We thus proposed, as a working hypothesis, that trilled song segments in song sparrows will achieve higher performance levels than nontrilled song segments.

METHODS

Song Sample

Songs of swamp and song sparrows used in this analysis were recorded from banded populations in western Massachusetts, U.S.A. (in Hampshire and Franklin counties). Chipping sparrow songs were obtained from the same region from both banded and unbanded populations, with supplementary recordings obtained from the Macaulay Library at the Cornell Lab of Ornithology (Ithaca, NY, U.S.A.). Field recordings were made using Marantz PMD660 digital recorders (sample rate 44.1 kHz) and Sennheiser directional microphones (ME66) or omnidirectional microphones (ME62) mounted in Telinga parabolas. Some of these recordings were obtained in prior studies (Goodwin & Podos, 2014; Lahti et al., 2011; Moseley et al., 2013). Swamp sparrow and chipping sparrow songs are composed of single trills; song sparrow songs include trills interspersed with note complexes (Marler & Peters, 1987; illustrated in Fig. 1). For each song sparrow song, we chose the longest-duration trill and the longest-duration note complex within each song for analysis. Some song sparrow trills start at a slow pace; in such cases, we only measured in our analyses the final, temporally consistent segment of the trill (e.g. Fig. 1e, opening trill, final three syllables only). The three focal species vary in song type repertoire sizes: individual chipping sparrows sing only a single song type; swamp sparrows sing between two and five song types, and song sparrows sing about 12–15 song types. Our sample size was as follows: chipping sparrows, 54 birds, 54 song types; swamp sparrows, 12 birds, 34 song types; song sparrows, 6 birds, 13 song types. This listing of song type sample size does not consider whether song types were shared among birds. We analysed three renditions of each song type for chipping and song sparrows, and one to five renditions of each song type for swamp sparrows. Performance values measured from multiple renditions per bird of the same song type were averaged prior to further statistical assessment.

Calculating Vocal Deviation

We calculated vocal deviations from swamp and chipping sparrow songs, and from trilled segments of song sparrow songs, using established methods (Huber & Podos, 2006; Moseley et al., 2013; Podos, 1997, 2001). In brief, for each trill type from each

bird, we calculated, using Signal 4.0 (Beeman, 2002), two parameters: (1) trill rate (Hz) as the number of syllables produced per second, measured from waveforms and spectrograms using an on-screen cursor; and (2) frequency bandwidth (kHz), that is, the difference between maximum and minimum frequencies, as measured from amplitude spectra at -24 dB relative to the trill's peak amplitude (illustrated in Podos, 1997; see also Zollinger, Podos, Nemeth, Goller, & Brumm, 2012). We then calculated the orthogonal distance of each trill to two family-wide upper-bound regressions of trill rate (Hz) by frequency bandwidth (kHz). The first of these upper-bound regressions was calculated using a standard method, in which sample data were parsed into x-axis bins of equal width, and maximal values per bin used for the regression calculation ($y = -0.124x + 7.55$; Podos, 1997). The second upper-bound regression was calculated using a 90% quantile regression method, which aims to avoid biases associated with skewed sample distributions (G. Beckers, C. ten Cate, & E. Meelis, personal communication; Wilson et al., 2014; $y = -0.089x + 5.96$ for the data set from Podos, 1997). Results from analyses using both upper-bound regressions were highly similar, as indicated in several ways, including very strong correlations between vocal deviation values calculated by the standard and quantile methods (chipping sparrows, $r = 0.977$; swamp sparrows, $r = 0.996$, song sparrows, $r = -0.995$; all $P < 0.001$). For the remainder of the paper we report vocal deviation data based only on the first method.

Calculating Frequency Excursion

Frequency excursion ('FEX') was calculated using an original open-source Linux program, 'FEX calculator' (see Supplementary Material for program code, operational notes and program Web site). FEX calculator queries users for three input parameters: (1) frequency filter values (to filter out extraneous noise above or below those of interest); (2) the selected amplitude threshold value (dB below peak threshold), below which sound energy in each clip is excluded in peak frequency calculations; and (3) fft sample size (number of samples per time bin). For all of our analyses here, we applied a frequency filter to exclude input below 1.25 kHz or above 10 kHz, an amplitude threshold value of -24 dB relative to the segment's peak frequency (the same threshold used for our vocal deviation calculations), and an fft value of 256 points (which allows a frequency resolution of 0.172 kHz for audio clips with a standard 44.1 kHz sample rate). Applied to an input sound clip, FEX calculator generates a spectrogram (Fig. 2a) indicating all points above the dB threshold (Fig. 2b) with peak frequency value points overlaid (Fig. 2c). While most of these points map cleanly onto song notes, others appear in the intervening silences between notes, or occasionally correspond to background sounds or noise. FEX calculator allows users to zoom in and delete 'false' bin points as assessed by eye (i.e. points that appear to correspond to background noise or other sources besides the focal signal). FEX calculator then calculates and sums the linear distances, on the spectrogram, between temporally adjacent points, including those that span silent intervals (Fig. 2d). This value, standardized for time (divided by the total signal time considered) is the frequency excursion value. Frequency excursion values were calculated only for six syllables within (the middle portions of) chipping sparrow and swamp sparrow trills, and calculated across the full temporally stable duration of song sparrow trills.

Question 1: How Do Frequency Excursion and Vocal Deviation Compare as Measures of Vocal Performance?

For each of the three species, we calculated and tested the significance of correlations between frequency excursion and vocal
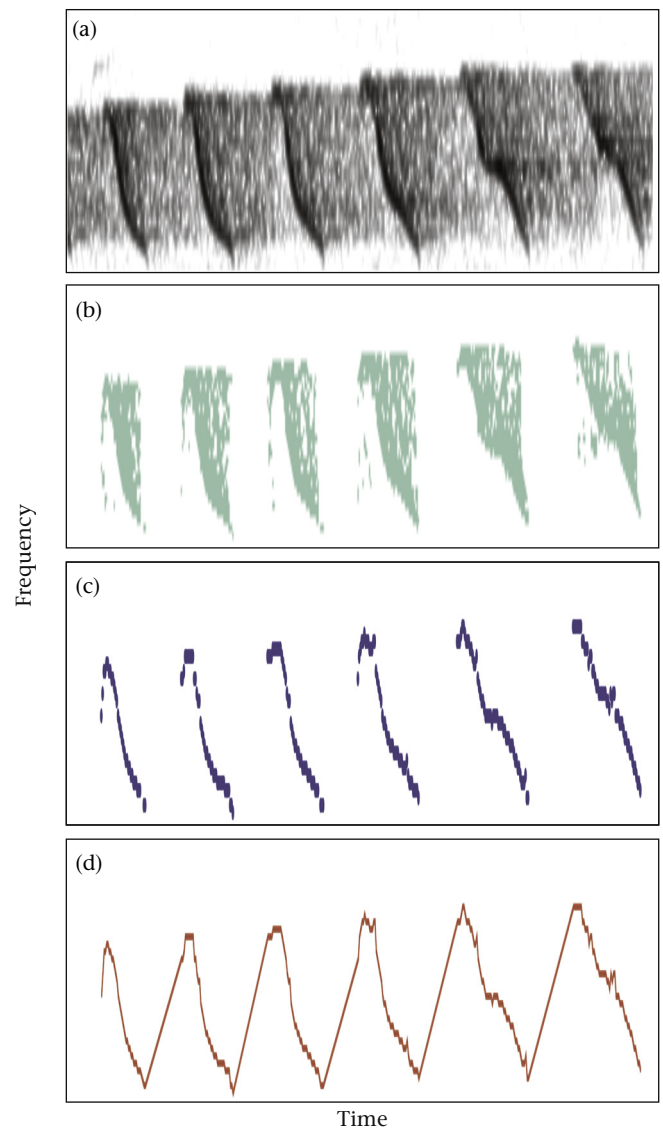

Figure 2. Plots illustrating how frequency excursion is calculated, for a single song clip, in FEX calculator. (a) Greyscale spectrogram of song segment from a male Adelaide's warbler, *Setophaga adelaidae*, recording courtesy of David Logue. The clip is 0.65 s long, and the *Y* axis shown (zoomed in here for illustration purposes) ranges from 2.05 to 8.03 kHz. (b) All points from the same clip with energy above our dB threshold, and thus eligible to be included in the frequency excursion calculation. Note that most but not all background noise is excluded in this step. (c) Highest-amplitude points per time bin, after manual deselection of candidate highest-amplitude points (identified by us, the user) as having captured noise or internote intervals rather than actual vocal output. (d) Highest-amplitude points connected by line segments. The cumulative length of the line segments divided by total time interval is the frequency excursion value. For this song segment, the cumulative path length is 45.17, segment duration (first to last highest-amplitude points) is 0.607 s, and the resulting frequency excursion value is 74.42.

deviation. Note that these calculations excluded nontrilled sequences in song sparrows, as vocal deviation cannot be calculated for nontrills. We expected correlations between vocal deviation and frequency excursion to be negative, given that higher performance songs should correspond to lower vocal deviation values (i.e. shorter distances from the upper-bound maxima) and higher frequency excursion values. Next, in a qualitative exercise, we plotted frequency excursion as a function of vocal deviation, overlaid linear regressions, and then assessed the position of sample points relative to the regression line. We expected that position on these plots

relative to the regression line would correspond to a trill's fine-scale phonological structure, especially in terms of the extent and/or rapidity of fine-scale frequency modulations. In particular we expected that trills with the abrupt and rapid modulations (within-notes) and transitions (between notes), both attributes invisible to vocal deviation, would be positioned above the regression line, whereas trills with relatively smooth frequency modulations and transitions would appear below the regression line.

Question 2: For Repertoire Species, What Are the Relationships Between Vocal Performance and Song Type Sharing?

This analysis focused on swamp sparrows, which in our sample featured some song types that were shared by two or more birds (with sharing determined by visual assessment of spectrograms). We calculated, for each song type sung by each bird, our two indices of vocal performance. Next, for each bird and song type, we calculated index means, standard errors and coefficients of variation (CV).

We then assessed, via ANOVA, the relative contributions of song type versus bird (i.e. within-individual versus between-individual factors) to variation in each metric of vocal performance. We also calculated eta^2 effect sizes for song type and for bird, for each vocal performance index. We expected that variation would be detected at both bird and song type levels and that, as with dark-eyed juncos (Cardoso et al., 2009), we would observe more variation between song types than between birds (within song types).

Finally we assessed, using Spearman rank correlations, the relationship between the mean vocal performance of different song types (as measured by both indices) and the number of birds in our sample who shared those song types. We calculated song sharing in two ways: (1) narrowly, within our sample of analysed songs only; and (2) broadly, including additional birds from our population whose songs were not analysed here. Our hypothesis, as outlined in the Introduction, was that song types with greater sharing would achieve higher performance levels than song types with less sharing.

Question 3: How Does Vocal Performance Vary in Trilled versus Nontrilled Song Sequences?

This analysis focused on our song sparrow sample, a species whose songs contain both trilled and nontrilled song sequences. For each song analysed, we calculated frequency excursion from one note complex and one trilled sequence. There were a number of decisions we had to make when calculating frequency excursion for note complexes. First, we only focused on segments of note complexes that appeared in multiple renditions of songs. This was necessary given that song sparrows regularly omit some segments from their note complexes across multiple renditions of a given type (Podos et al., 1992). Second, when perusing song sparrow songs for these analyses, we noted an unexpectedly large proportion of songs that featured double-voicing, in which two fundamental frequencies are voiced simultaneously. While this is a potentially important aspect of vocal performance, our frequency excursion metric is not able to account for this axis of performance, given that calculating frequency excursion requires selection of a single peak frequency per time bin. We thus excluded songs with double-voicing from our sample. Third, we opted to omit buzzes in our calculations of note complex frequency excursion. Most note complexes include buzzes, defined as having amplitude modulation rates of 35 Hz or greater, and being produced via pulsatile rather than minibreath respiration (e.g. Hartley & Suthers, 1989). For each note complex with one or more buzzes, we calculated frequency excursion for all song segments before, after and

between buzzes, and then generated a composite frequency excursion value for each note complex as the sum of all resulting path lengths divided by the sum of all resulting durations.

We tested for statistical differences between trilled and non-trilled song sequence categories using a repeated measures *t* test. We predicted, as outlined in the Introduction, that the performance of trilled song sequences would exceed the performance of non-trilled song sequences.

RESULTS

Frequency Excursion versus Vocal Deviation

The three species examined here differed widely in vocal deviation, with chipping sparrows achieving the highest performance (mean $\pm$ SD vocal deviation scores = 1.54 $\pm$ 0.76, $N = 54$), followed by swamp sparrows (2.43 $\pm$ 0.58, $N = 34$) and then by song sparrows (3.42 $\pm$ 1.26, $N = 13$; ANOVA: $F_{2,12} = 35.26$, $P < 0.001$; all Tukey HSD: $P < 0.001$). By contrast, as measured by frequency excursion, chipping and swamp sparrows achieved roughly the same vocal performance levels, while song sparrows retained their lowest-performance rank (chipping sparrows: 146.0 $\pm$ 42.8, $N = 54$; swamp sparrows: 149.4 $\pm$ 47.0, $N = 34$; song sparrows: 83.0 $\pm$ 30.5, $N = 13$; ANOVA: $F_{2,12} = 12.73$, $P < 0.001$; Tukey HSD for chipping $\times$ song sparrow and swamp $\times$ song sparrow: $P < 0.001$; Tukey HSD for chipping $\times$ song sparrow: $P > 0.5$).

For all three species, our two vocal performance indices correlated negatively with each other, as expected (Pearson's product-moment correlation: chipping sparrows: $r_{52} = -0.64$, $P < 0.001$; swamp sparrows: $r_{32} = -0.60$, $P < 0.001$; song sparrows: $r_{11} = -0.65$, $P = 0.016$). The strength of the correlation in swamp sparrows was lessened yet retained statistical significance when we removed one notable high-performance outlier ($r_{31} = -0.43$, $P = 0.012$). In Fig. 3 we present plots comparing values generated by the two performance indices. Songs on this plot above the regression lines tend to have features that we presume require high vocal performance. Such features include rapid frequency modulations and large frequency jumps between the end and start of successive notes (e.g. Fig. 1a, c). By contrast, songs below the regression lines tended to show more gradual frequency modulations both within and between notes (e.g. Fig. 1b, d).

Vocal Performance Variation and Song Type Sharing

Our sample of swamp sparrows and their song types showed wide variation in performance by both bird and song type (Table 1). Of the two performance indices, frequency excursion proved better able to discern variation among the two factors analysed (birds and song types). This is shown in our results in two ways. First, an ANOVA based on vocal deviation (Table 2) failed to identify significant contributions by either factor to sample-wide vocal performance variation, whereas an ANOVA based on frequency excursion (Table 2) revealed significant contributions of song type. Second, inspection of effect sizes suggests that song type is a greater contributor than individual bird to the overall sample variation in performance, with this difference being more pronounced for frequency excursion (Table 2). These outcomes are consistent with the expectation that song types are more important than individual birds in defining a population's overall vocal performance variation (Cardoso et al., 2009).

Frequency excursion also revealed greater differences among factors for our coefficient of variation (CV) data: vocal deviation identified similar ranges of performance variation within birds (mean CV value of 22.10) and song types (mean CV = 19.19; Table 1). By contrast, frequency excursion identified substantially
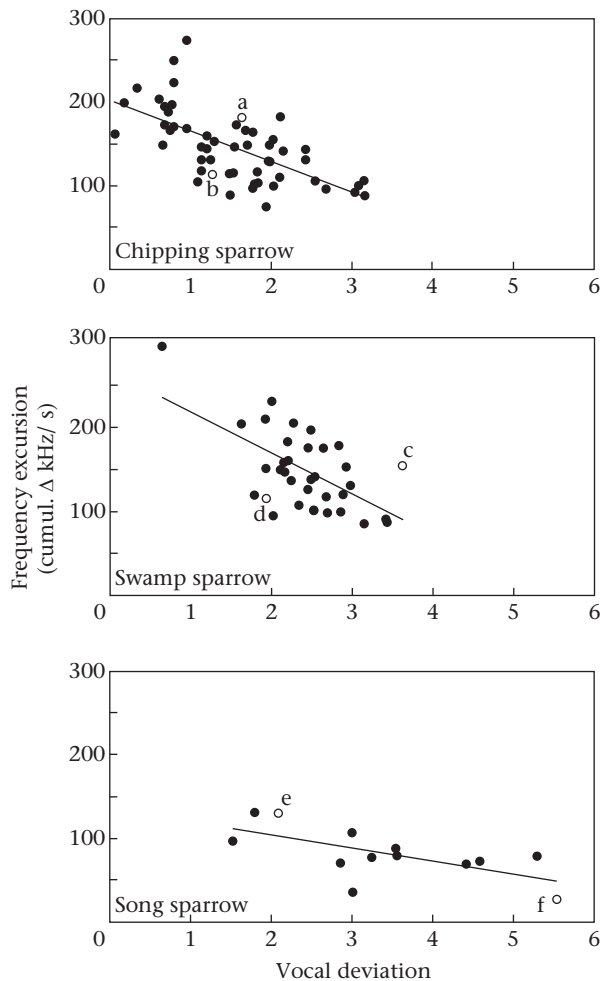
Figure 3. Frequency excursion as a function of vocal deviation for our three study species. Song types with open circles and labels (a–f) are those illustrated in Fig. 1. For song types above the regression lines (e.g. a, c, e), vocal performance as measured by frequency excursion exceeded that predicted by vocal deviation alone, whereas song types below the regression lines (e.g. b, d, f) fell short of performance levels predicted by vocal deviation alone.

higher CV values within birds (mean CV = 27.21) than within song types (mean CV = 16.69; Table 1). This provides another line of support for the hypothesis that vocal performance within types varies less than vocal performance within birds.

Both performance indices covaried with song type sharing, yet in the direction opposite to that predicted: song types shared by more birds were characterized by lower vocal performance. When we measured song sharing within samples only (Fig. 4, left panels), the relationship approached statistical significance with the vocal deviation index (Spearman rank correlation: $r_S = 0.543$, $F_{1,11} = 130.73$, $P = 0.068$), and achieved statistical significance with the frequency excursion index ($r_S = -0.690$, $F_{1,11} = 483.32$, $P = 0.013$). When we measured song sharing across the population at large (Fig. 4, right panels), the relationship achieved statistical significance with both performance indices (vocal deviation: $r_S = 0.465$, $F_{1,11} = 119.88$, $P = 0.048$; frequency excursion: $r_S = -0.508$, $F_{1,11} = 455.19$, $P = 0.043$).

Trilled versus Nontrilled Song Sequences

In Fig. 5 we present, from our song sparrow sample, a summary of frequency excursion values for both trilled and nontrilled song

sequences. Frequency excursion values in nontrilled song sequences exceeded those from trilled song sequences, as predicted, although not at a level that was statistically significant (repeated measures t test: $t_{11} = 1.131$, $P = 0.282$).

DISCUSSION

Our two main goals in this paper were to introduce the frequency excursion index and to apply it to representative questions about vocal performance. A key attribute of our frequency excursion index is that it characterizes not just frequency modulations within notes, but also frequency transitions between notes, that is, during the silent gaps in song. As such, frequency excursion builds on the suggestion of Podos et al. (2009, their Figure 1) and parallels a method developed by Geberzahn and Aubin (2014) to quantify vocal performance in skylarks, *Alauda arvensis*. While we here apply the frequency excursion method to songbird songs, we note that it could be applied readily to other taxa and vocalizations of interest.

Before discussing our data and analyses, it is worth emphasizing that frequency excursion is not suited to capture all potentially significant aspects of vocal performance. A first such example concerns modulations in amplitude, with broader amplitude modulations or the ability to sing at consistently high amplitudes likely indicating higher vocal performance (Forstmeier et al., 2002). Frequency excursion also cannot be applied to the analysis of nontonal sounds, in which peak frequencies cannot be identified with confidence within each time bin. It thus cannot be applied readily to analysis of buzzes, harmonic stacks, two-voiced sounds or other complex vocal phenomena that are likely to challenge singers' performance limits (e.g. Fee, Shraiman, Pesaran, & Mitra, 1998). The frequency excursion index also maintains, in its construction, at least four implicit assumptions about vocal mechanics: (1) more extensive frequency modulations both within and between notes require higher levels of performance; (2) frequency modulations within and between notes can be scaled for performance equivalently, using identical frequency by time parameters; (3) frequency up-sweeps and down-sweeps present equivalent and thus directly comparable production challenges; and (4) the performance required for frequency modulations varies linearly across the frequency scale. These assumptions are likely oversimplified, and we welcome user-guided adjustments and reweightings in how FEX is calculated. As an illustration, consider the fourth assumption above. Our decision to use a linear scale to code frequency for our FEX calculations was motivated mainly by an interest in retaining a common scale with spectrograms, which employ linear frequency scales and on which visual descriptions of FEX calculations can be overlaid (Fig. 2). However, as was recently argued by Cardoso (2013b), performance indices involving frequency comparisons (including both FEX and VDEV) might also be conducted using frequency data that is first log transformed, in part because use of linear frequency scales might overestimate vocal performance at higher frequencies. If, to illustrate, doubling a source frequency requires similar performance across the frequency scale, then a bird modulating its song from 2 kHz to 4 kHz would receive four times the performance 'credit' as compared to a transition from 0.5 kHz to 1 kHz. Ideally, decisions about whether to log transform frequency data before calculating performance values will be guided not just by theory but also by empirical studies that explore relationships between vocal mechanics and song frequency variation (e.g. Goller & Suthers, 1996; Hoese et al., 2000; Nelson, Beckers, & Suthers, 2005; Riede et al., 2006). In any case, to facilitate further exploration of the outcomes of linear versus log-transformed frequency scaling, we offer users a log-transformation option in FEX calculator.

Table 1
Performance scores (vocal deviation, frequency excursion) by song type and bird ID for our swamp sparrow sample.

Song type	Bird ID 1	2	3	4	5	6	7	8	9	10	11	12	Mean	SD	CV
Vocal deviation															
A	1.92												1.92		
B			2.52					2.02	2.86				2.47	0.42	17.1
C						2.2		3.42		2.02			2.55	0.76	29.9
D	2.67		2.54	2.15					2.69				2.51	0.25	10.0
E		1.78		2.35		3.15	1.94						2.31	0.61	26.6
F		2.01						2.64					2.33	0.45	19.2
G		2.15					2.98	3.42					2.85	0.64	22.6
H					2.12		2.45					2.16	2.24	0.18	8.0
I		2.49	2.92	3.32	1.93								2.67	0.60	22.4
J						1.63			2.27		2.84		2.25	0.61	26.9
K	2.49		2.46		2.89								2.61	0.24	9.2
L		0.64											0.64		
Mean	2.36	1.81	2.61	2.61	2.31	2.33	2.46	2.88	2.61	2.02	2.84	2.16			
SD	0.39	0.70	0.21	0.63	0.51	0.77	0.52	0.68	0.30						
CV	16.6	38.9	8.0	24.0	22.0	33.0	21.2	23.6	11.7						
Frequency excursion															
A	211.2												211.24		
B			102.6					96.1	101				99.89	3.36	3.37
C						184.5		87.2		170.6			147.42	52.60	35.68
D	118.3		142.8	147.2					99.7				127.01	22.19	17.47
E		120.6		108.1		86.0	116.4						107.79	15.43	14.31
F		232.1						176.0					204.07	39.65	19.43
G		159.6					132.5	92.2					128.11	33.91	26.47
H					150.7		127.8					142.2	140.22	11.55	8.23
I		197.7	153.8	146.0	152.4								162.49	23.73	14.61
J						205.6			206.8		179.1		197.16	15.67	7.95
K	139.5		176.8		121.3								145.87	28.29	19.39
L		297.7											297.71		
Mean	156.4	201.6	144.0	133.8	141.4	158.7	125.6	112.9	135.8	170.6	179.1	142.2			
SD	48.7	68.0	31.0	22.2	17.5	63.9	8.3	42.2	61.4						
CV	31.1	33.8	21.6	16.6	12.4	40.2	6.6	37.4	45.2						

Descriptive statistics (mean, standard deviation and coefficients of variation) are shown in the final three columns and rows. Mean CVs were as follows: vocal deviation × bird = 22.10; vocal deviation × song type = 19.19; frequency excursion × bird = 27.21; frequency excursion × song type = 16.69.

Table 2
Two-way ANOVA (type III) results and effect sizes for swamp sparrow data, for our two performance indices

Factor	df	SS	F	P	Eta^2 Vocal deviation	Frequency excursion
Vocal deviation						
Bird	11	3.174	1.191	0.388		
Song type	11	4.347	1.631	0.215		
Residuals	11	2.665				
Frequency excursion						
Bird	11	10 321	1.931	0.145		
Song type	11	43 586	8.155	<0.001		
Residuals	11	5345				
Effect sizes						
Bird					0.302	0.142
Song type					0.413	0.597

Returning to the present analyses: the first main question we asked was how the frequency excursion and vocal deviation indices compare as measures of vocal performance. The generally strong relationships between the two performance indices suggests that they overlap in aspects of vocal performance that they capture. However, inspection of the phonological structure of songs, with reference to regression plots (Fig. 3), illustrates how frequency excursion indeed captures additional, finer-scale aspects of vocal performance. In particular, songs that map above the regression lines tend to have relatively rapid frequency modulations and large frequency jumps between notes, features that are overlooked by vocal deviation (e.g. Fig. 1a, c). By contrast, songs with slower, more gradual frequency modulations and less abrupt frequency transitions between notes map comparatively low in frequency excursion (Fig. 1b, d).

Both of our indices revealed species differences in vocal performance. Following vocal deviation, chipping sparrows sang with the highest performance, swamp sparrows with intermediate performance and song sparrows with the lowest performance. Frequency excursion also places song sparrows as the poorest performers, but lumps chipping sparrows and swamp sparrows as equivalent performers. These results correspond roughly to body size, with the smallest-bodied species achieving the highest performance. This contrasts with the results of a larger analysis of
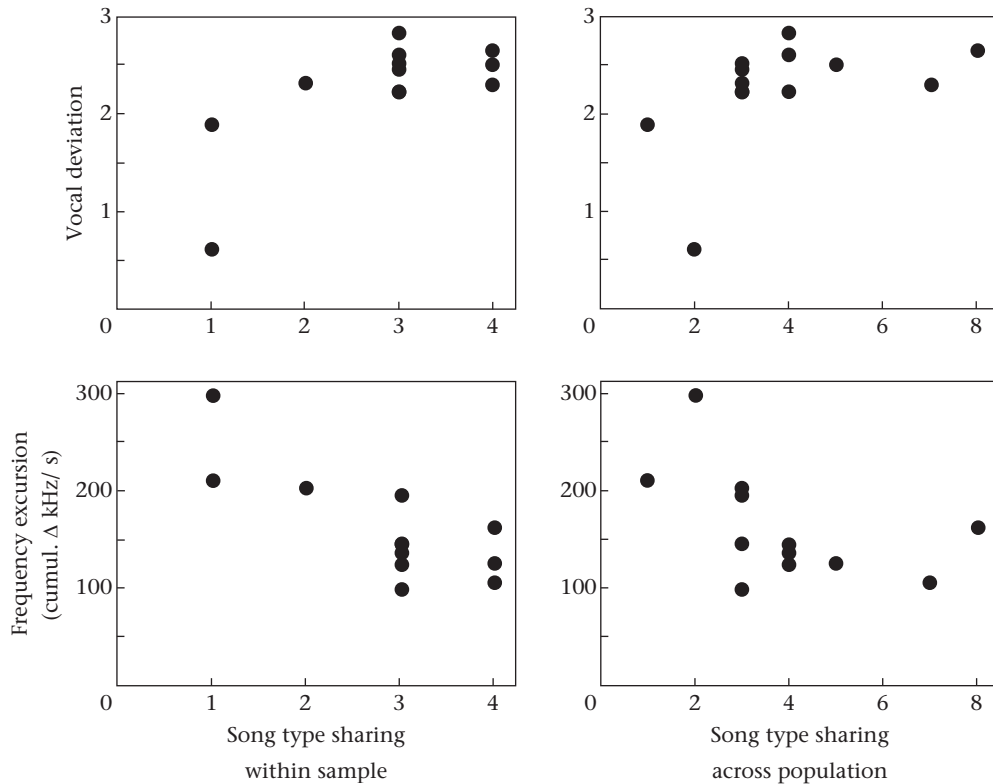
Figure 4. Average vocal performance of swamp sparrow song types plotted against the number of birds in our sample who shared those types. Left panels show data when song sharing was calculated within the sample only, and right panels show data when song sharing was calculated across the population at large. In all cases, vocal performance declined as the incidence of song sharing increased. The relationship approached statistical significance for the upper left panel data, and achieved statistical significance for the other three panels (see text). The direction of the observed relationship contradicts our expectation that shared song types should require higher performance.
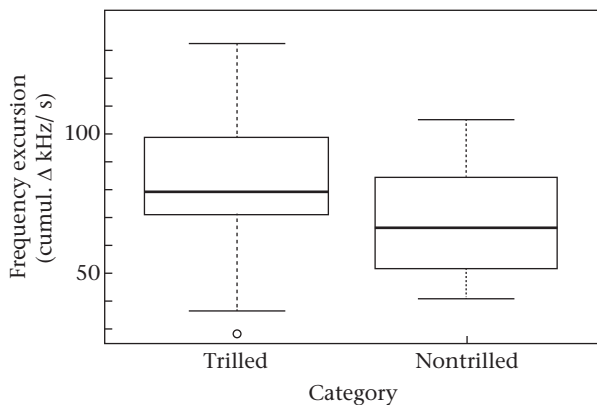

Figure 5. Frequency excursion values for trilled and nontrilled song sequences from our song sparrow sample. Values shown are medians, first and third quartiles, non-outlying minima and maxima, and one outlier.

multiple sparrow species, which failed to identify a body size effect on vocal deviation (Podos, 2001). Species differences in vocal performance might also arise from varying strengths of sexual selection on vocal attributes. Consistent with this possibility are data showing that both chipping and swamp sparrows attend to inter-male variation in vocal performance (as measured by trill rate or vocal deviation; Goodwin & Podos, 2014; Moseley et al., 2013), whereas in song sparrows, song assessment seems based mainly on nonperformance features such as song type matching and soft song (Searcy, Akçay, Nowicki, & Beecher, 2014). With this latter point, we acknowledge that further work would be needed with song

sparrows to test directly the potential salience of vocal performance features in song assessment.

The next set of questions focused on song repertoires and song type sharing in swamp sparrows. Swamp sparrows learn to sing by imitation, copying adults on their natal grounds (Marler & Peters, 1982; Mowbray, 1997). Birds who share song types likely learn those types from different tutors, yet the structure of notes and song types tends to be conserved across the species range (Marler & Pickert, 1984). For this reason, song performance would seem likely to be more restricted within type than across types (within birds). Indeed, our results here parallel those of Cardoso et al. (2009) for dark-eyed juncos: the frequency excursion index varied significantly by song type but not by bird, with the effect size of song type being notably larger. Notably, these distinctions were not detected by the vocal deviation metric. To the extent that song types are less variable than individuals in vocal performance, the value of individual songs as indicators of signaller attributes related to vocal capacity should be compromised (Cardoso et al., 2009). However, our analysis did not take into account song type use (i.e. whether birds tend to use songs with different performance levels in different singing contexts).

We also detected relationships between song sharing and vocal performance, in the direction opposite to that expected (and again with stronger effects for frequency excursion). Overall, songs that were shared tended to be of lower performance, and our initial assumption that song sharing would promote the evolution of higher performance (Logue & Forstmeier, 2008; see also Poesel & Nelson, 2015) is thus unsupported. Perhaps the unshared, higher performance songs are used rarely and reserved for the most critical social interactions. Moreover, if young birds are unable to produce high-performance song types with accuracy, then perhaps

they will preferentially crystallize lower-performance songs, which would increase the prevalence of low-performance songs in a population and, correspondingly, the likelihood that they would be shared. Of particular interest in future work will be attention to the interplay of song performance and song use in species like swamp sparrows that have song repertoires (as in Cardoso, Atwell, Hu, Ketterson, & Price, 2012; DuBois et al., 2011).

In a final sample application, we asked whether frequency excursion values were greater for trilled than nontrilled components of song sparrow songs. While frequency excursion values were greater for trilled as compared to nontrilled song segments, in the predicted direction, this difference was not statistically significant. It thus seems that song sparrows do not achieve higher performance in trills, at least as measured by frequency excursion. One possible explanation for this outcome is that selection on trill performance in song sparrows might be comparatively weak, at least as compared to our other two study species, for which available data suggests that trills are both mechanically limited and scrutinized in field contexts. Further studies comparing the performance of trilled versus nontrilled songs or song segments should include additional species, particularly those with evidence for relying on performance variation in vocal communication. Nightingales, *Luscinia megarhynchos*, would seem like a particularly good candidate species, given that they seem to sing with high performance and also produce both trilled and nontrilled song segments (Kunc, Amrhein, & Naguib, 2006).

Overall, we envision frequency excursion being applied to these and other questions about vocal performance, including questions previously addressed using other performance measures such as trill rate and vocal deviation. Some such questions concern the relationship between ecology, morphology and vocal signal structure (e.g. Ballentine, Horton, Brown, & Greenberg, 2013; Derryberry et al., 2012; Podos, 2001; Seddon, 2005; Slabbekoorn & Smith, 2000); whether vocal performance offers a reliable indicator of signaller attributes (e.g. Goodwin & Podos, 2014; Juola & Searcy, 2011; Moseley et al., 2013) and the extent of vocal performance variation expressed in nature (Cardoso & Hu, 2011; Lambrechts, 1997; Podos, 1997; Wilson et al., 2014).

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.03.036.

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