A Fine-Scale, Broadly-Applicable Index of Vocal Performance: Frequency Excursion

Jeffrey Podos¹, Dana L. Moseley², Sarah E. Goodwin³, Jesse McClure⁴, Benjamin N. Taft⁵, Amy V. H. Strauss³, Christine Rega-Brodsky⁶, David C. Lahti⁷

1. Department of Biology, Graduate Program in Organismic & Evolutionary Biology, University of
Massachusetts, Amherst MA

2. Environmental Science Program, College of William & Mary, Williamsburg VA

3. Graduate Program in Organismic & Evolutionary Biology, University of Massachusetts, Amherst MA

4. Program in Bioinformatics and Integrative Biology, University of Massachusetts Medical School,
Worcester MA

5. Landmark Acoustics, LLC, Racine, WI

6. University of Missouri, Department of Fisheries & Wildlife Sciences, Columbia, MO

7. Department of Biology, Queens College, City University of New York, New York, NY

Corresponding author: Jeffrey Podos, Department of Biology, University of Massachusetts, Amherst MA
01003, jpodos@bio.umass.edu, 413-545-0847 (phone)

Word count: 5466

22 ABSTRACT

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

41

42 Key words: vocalizations, bird song, vocal performance, vocal deviation, frequency
43 excursion, chipping sparrow, swamp sparrow, song sparrow

44 INTRODUCTION

45 Much research in the fields of sexual selection and animal communication has focused
46 on mating signals and displays, produced by animals as they compete for access to
47 prospective mates (Andersson 1994; Searcy & Nowicki 2005; Seyfarth et al. 2010;
48 Bradbury & Vehrencamp 2011). Some mating displays seem to require high vigor or
49 skill to be performed effectively (Darwin 1871; Byers et al. 2010). As such, only the
50 “best” signalers in a population should be able to execute the most complex or
51 challenging displays, rendering these displays reliable as indicators of signaler quality
52 (Byers et al. 2010; Cardoso 2013a). Empirical evidence available to date, while limited,
53 suggests that variation in display performance can indeed hold functional value, both to
54 males assessing potential competitors and to females assessing prospective mates
55 (e.g., Arak 1983; Vehrencamp et al. 1989; Welch et al. 1998; Barske et al. 2011;
56 Wilgers & Hebets 2011; Reichert & Gerhardt 2012; Zanollo et al. 2013).

57 Useful recent insights into display performance variation and its functional
58 consequences have emerged through studies of vocal displays in vertebrates, including
59 song in songbirds (e.g., Nowicki et al. 1998; Byers 2007; Podos et al. 2009; Spencer &
60 McDougall-Shackleton 2011; Sakata & Vehrencamp 2012). Songbirds sing using
61 multiple motor systems, namely the syrinx (sound source), respiratory system, and
62 vocal tract (reviewed by Suthers 2004; Podos & Nowicki 2004; Podos et al. 2009; Riede
63 & Goller 2014). Performance challenges arise as birds coordinate syrinx modulations
64 with intricately patterned respiratory movements, and as they track changing source
65 frequencies via precise reconfigurations of the vocal tract (Westneat et al. 1993; Hoese

et al. 2000; Podos et al. 2004b; Riede et al. 2006; Suthers et al. 2012). 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 et al. 2004a; Zollinger & Suthers 2004; see also Lahti et al. 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., Thorpe & Lade 1961; Podos 1997; Figure 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 tradeoff 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., Price & Lanyon 2004; Beebee 2004; Ballentine et al. 2004; Illes et al. 2006; Cramer & Price

2007; Cardoso et al. 2007; Liu et al. 2008; Janicke et al. 2008; Sockman 2009; Cardoso & Hu 2011, Juola & Searcy 2011; Pasch et al. 2011; Derryberry et al. 2012; see also Wilson et al. 2014).

Descriptions of trill rate and frequency bandwidth, and of tradeoffs 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 graph a trill sequence of interest on a taxon-wide plot 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 (Podos 2001; Ballentine et al. 2004). The resulting distance, termed “vocal deviation”, corresponds inversely to presumed vocal performance requirements: higher vocal deviations are indicative of low performance songs, and vice versa. 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 (Podos 2001; Huber & Podos 2006; Ballentine 2006; Sockman 2009; Derryberry et al. 2012), body mass and age (Ballentine 2009), the vigor of solicitation displays or strength of spatial preference by females (Ballentine et al. 2004; Caro et al. 2010; see also Draganoiu et al. 2002), the strength and direction of song playback responses by territorial males (Illes et al. 2006; Cramer & Price 2007; DuBois et al.

2011; Moseley et al. 2013; see also de Kort et al. 2009; Goodwin & Podos 2014), and body condition or reproductive success (Janicke et al. 2008; Juola & Searcy 2011).

While vocal deviation has been widely-used 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 impact 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., Podos et al. 2009, their Fig. 1; see also Geberzahn & Aubin 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 (Geberzahn & Aubin 2014; Cardoso 2014). While many species trill, others do not and at present we have no clear guideline for quantifying non-trilled song performances, or for comparing performances of songs with trilled versus non-trilled 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 spectrograph 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 inter-note and inter-syllable intervals, and standardize this summed distance to a per-second basis. Frequency excursion thus provides a cumulative assessment of frequency modulation rates across the course of an entire song or song segment. As in Gerberzahn & Aubin (2014), frequency excursion accounts for the vocal 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 Westneat et al. 1993; Podos et al. 2004b; Cardoso 2014). 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 (JM) has written to facilitate the measurement of frequency excursion (Appendix 1). 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 calculate correlations between vocal deviation and frequency excursion, and ask how songs' distributions on regression plots correspond to their spectrographic structure. Following the logic presented above, we expect that frequency

excursion will provide a more precise accounting of within-syllable vocal performance, as inferred from spectrograms and based on assumptions about vocal mechanics. We next ask, 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 et al. (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 expect that performance variation within the repertoires of individual swamp sparrows will exceed performance variation within shared song types (Cardoso et al. 2009). In our swamp sparrow sample we also compare performance levels of shared versus unshared song types. We predict that the vocal performance of shared song types will 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 & Nelson (2015) have shown that vocal performance (*sensu* Forstmeier et al. 2002) is higher for shared than unshared song types in Puget Sound white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). Finally we ask, within our song sparrow sample, whether performance levels in trilled song sequences exceed those in non-trilled song sequences. This test is possible in song sparrows given that their songs include both trilled and non-trilled segments (Figure 1). Trill structure in numerous species has been shown to be subject to performance constraints (e.g., Podos 1996; Zollinger & Suthers 2004; Suthers et al.

2012), and trills may thus be particularly well suited to reveal variation among males in their performance abilities (e.g., Brumm & Slater 2006; Logue & Forstmeier 2008; Schmidt et al. 2008; Cardoso 2013a; Petruskova et al. 2014). By contrast, limited data are available regarding the performance levels of non-trilled songs. We thus propose, as a working hypothesis, that in song sparrows, trilled song segments will achieve higher performance levels than non-trilled song segments.

METHODS

Song sample

Songs of swamp and song sparrows used in this analysis were recorded from banded populations in Western Massachusetts (Hampshire and Franklin County MA). Chipping sparrow songs were obtained from the same region from both banded and un-banded populations, with supplementary recordings obtained from the Macaulay Library at the Cornell Lab of Ornithology. 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 (Lahti et al. 2011, Moseley et al. 2013, Goodwin & Podos 2014). Swamp sparrow and chipping sparrow songs are comprised 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 3 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 2 and 5 song types, and song sparrows sing about 12 to 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 analyzed 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

Vocal deviations from swamp and chipping sparrow songs, and from trilled segments of song sparrow songs, were calculated using established methods (Podos 1997, 2001; Huber & Podos 2006; Moseley et al. 2013). 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) i.e., 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 et al. 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 pers. comm., 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 Appendix 1 for program code, operational notes, and program website). 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 (# 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 6 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 deviation. Note that these calculations excluded non-trilled sequences in song sparrows, as vocal deviation cannot be calculated for non-trills. 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-squared 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, we would observe more variation between song types than between birds (Cardoso et al. 2009).

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: (i) narrowly, within our sample of analyzed songs only; and (ii) broadly, including additional birds from our population whose songs were not analyzed here. Our hypothesis, as outlined in the introduction, is 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 non-trilled song sequences?

This analysis focused on our song sparrow sample, a species whose songs contain both trilled and non-trilled song sequences. For each song analyzed 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 of 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 without double-voicing from our sample. Third, we opted to omit buzzes in our note complex frequency excursion calculations. Most note complexes include buzzes, defined as having amplitude modulation rates of 35 Hz or greater, and being produced via pulsatile rather than mini-breath 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 ± 0.76), followed by swamp sparrows (2.43 ± 0.58) and then by song sparrows ($3.42 \pm$

1.26; 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 ± 42.8 ; swamp sparrows 149.4 ± 47.0 ; song sparrows 83.0 ± 30.5 ; ANOVA $F_{2,12} = 12.73$, $P < 0.001$, Tukey HSD for chipping x song sparrow and swamp x song sparrow $P < 0.001$, Tukey HSD for chipping x song sparrow $P > 0.5$). For all three species, our two vocal performance indices correlated negatively with each other, as expected (chipping sparrows, $r = -0.64$, $p < 0.001$; swamp sparrows, $r = -0.60$, $p < 0.001$; song sparrows, $r = -0.65$, $p = 0.016$). The strength of the correlation in swamp sparrows is lessened yet retains statistical significance when we remove one notable high-performance outlier ($r = -0.43$, $p = 0.012$). In Figure 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., Figure 1A, C). By contrast, songs below the regression lines tended to show more gradual frequency modulations both within and between notes (e.g., Figure 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

analyzed (birds and song types). This is shown in our results in two ways. First, an ANOVA based on vocal deviation (Table 2A) failed to identify significant contributions by either factor to sample-wide vocal performance variation, whereas an ANOVA based on frequency excursion (Table 2B) 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 2C). 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 value of 19.19, Table 1A). By contrast, frequency excursion identified substantially higher CV values within birds (mean value of 27.21) than within song types (mean value of 16.69; Table 1B). 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-sample 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 non-trilled song sequences

In Figure 5 we present, from our song sparrow sample, a summary of frequency excursion values for both trilled and non-trilled song sequences. Frequency excursion values in non-trilled song sequences exceeded those from trilled song sequences, as predicted, although not at a level that was statistically significant (repeated measures t-test, $df=11$, $t=1.131$, $p=0.282$).

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, i.e. 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 & 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 non-tonal 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 all likely challenge singers' performance limits (e.g., Fee et al. 1998).

The frequency excursion index also contains, in its construction, at least four implicit assumptions about vocal mechanics: (i) more extensive frequency modulations both within and between notes require higher levels of performance; (ii) frequency modulations within and between notes can be scaled for performance equivalently, using identical frequency by time parameters; (iii) frequency up-sweeps and down-sweeps present equivalent (and thus directly comparable) production challenges; and (iv) the performance required for frequency modulations varies linearly across the frequency scale. These assumptions are likely oversimplified, and we welcome user-guided adjustments and re-weightings 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 gain 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 et al. 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.

Returning 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 indicates 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 and 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 poorer performers, but lumps chipping sparrows and swamp sparrows as equivalent performers. These results correspond roughly to body size, with the largest-bodied species achieving the lowest performance. This contrasts the results of a larger analysis of multiple sparrow species, which failed to identify a body-size effect on vocal deviation (Podos 2001). Species difference in vocal performance might also arise from varying strengths of sexual selection on vocal performance. 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, Moseley et al. 2013; Goodwin & Podos 2014), whereas in song sparrows, song assessment seems based mainly on non-performance features such as song type matching and soft song (Searcy et al 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 in this species.

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). 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 more 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 signaler 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 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 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 DuBois et al. 2011; Cardoso et al. 2012).

In a final sample application, we asked whether frequency excursion values were greater for trilled than non-trill components of song sparrow songs. While frequency

excursion values were greater for trilled as compared to non-trilled 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 non-trilled songs or song segments should include additional species, particularly those with evidence for relying on performance variation in vocal communication. Nightingales (*Luscinia megarhychos*) would seem like a particularly good candidate species, given that they seem to sing with high performance and also produce both trilled and non-trilled song segments (Kunc et al. 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., Slabbekoorn & Smith 2000; Podos 2001; Seddon 2005; Derryberry et al. 2012; Ballentine et al. 2013); whether vocal performance offers a reliable indicator of signaler attributes (e.g., Juola and Searcy 2011; Moseley et al. 2013; Goodwin & Podos 2014); and the extent of vocal performance variation expressed in nature (Lambrechts 1997; Podos 1997; Cardoso & Hu 2011; Wilson et al. 2014).

ACKNOWLEDGEMENTS

We thank the Massachusetts Department of Conservation and Recreation, and the Town of Amherst Conservation Committee, for granting access to field sites; Greg LeBoeuf, Chrissy Rivera, and Cosmo LaViola for assistance in the field; David Logue, Gail Patricelli, and two anonymous reviewers for insightful feedback on earlier drafts of the manuscript, and National Science Foundation for funding (NSF IOS 1011241 to DLM and JP, and NSF IOS 1311393 to SEG and JP).

LITERATURE CITED

- Andersson, M. B.** 1994. *Sexual Selection*. Princeton, N.J.: Princeton University Press.
- Arak, A.** 1983. Sexual selection by male male competition in natterjack toad choruses. *Nature*, 306, 261-262.
- Ballentine, B.** 2006. Morphological adaptation influences the evolution of a mating signal. *Evolution*, 60, 1936-1944.
- Ballentine, B.** 2009. The ability to perform physically challenging songs predicts age and size in male swamp sparrows, *Melospiza georgiana*. *Animal Behaviour*, 77, 973-978.
- Ballentine, B., Horton, B., Brown, E. T. and Greenberg, R.** 2013. Divergent selection on bill morphology contributes to nonrandom mating between swamp sparrow subspecies. *Animal Behaviour*, 86, 467-473.
- Ballentine, B., Hyman, J. and Nowicki, S.** 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, 15, 163-168.
- Barske, J., Schlinger, B. A., Wikelski, M. and Fusani, L.** 2011. Female choice for male motor skills. *Proceedings of the Royal Society B-Biological Sciences*, 278, 3523-3528.
- Beebee, M. D.** 2004. Variation in vocal performance in the songs of a wood-warbler: Evidence for the function of distinct singing modes. *Ethology*, 110, 531-542.
- Beeman, K.** 2002. *SIGNAL 4.0*. Belmont, MA: Engineering Design.

- 535 **Bradbury, J. W. and Vehrencamp, S. L.** 2011. *Principles of Animal Communication*. Sinauer
536 Associates.
- 537 **Brumm, H. and Slater, P. J. B.** 2006. Ambient noise, motor fatigue, and serial redundancy in
538 chaffinch song. *Behavioral Ecology and Sociobiology*, 60, 475-481.
- 539 **Byers, B. E.** 2007. Extrapair paternity in chestnut-sided warblers is correlated with consistent
540 vocal performance. *Behavioral Ecology*, 18, 130-136.
- 541 **Byers, J., Hebets, E. and Podos, J.** 2010. Female mate choice based upon male motor
542 performance. *Animal Behaviour*, 79, 771-778.
- 543 **Cardoso, G. C.** 2013a. Sexual signals as advertisers of resistance to mistakes. *Ethology*, 119,
544 1035-1043.
- 545 **Cardoso, G. C.** 2013b. Using frequency ratios to study vocal communication. *Animal*
546 *Behaviour*, 85, 1529-1532.
- 547 **Cardoso, G. C.** 2014. Studying the silent side of birdsong. *BMC Biology*, 12, 3.
- 548 **Cardoso, G. C., Atwell, J. W., Hu, Y., Ketterson, E. D. and Price, T. D.** 2012. No correlation
549 between three selected trade-offs in birdsong performance and male quality for a species
550 with song repertoires. *Ethology*, 118, 584-593.
- 551 **Cardoso, G. C., Atwell, J. W., Ketterson, E. D. and Price, T. D.** 2007. Inferring performance in
552 the songs of dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology*, 18, 1051-1057.
- 553 **Cardoso, G. C., Atwell, J. W., Ketterson, E. D. and Price, T. D.** 2009. Song types, song
554 performance, and the use of repertoires in dark-eyed juncos (*Junco hyemalis*). *Behavioral*
555 *Ecology*, 20, 901-907.
- 556 **Cardoso, G. C. and Hu, Y.** 2011. Birdsong performance and the evolution of simple (rather
557 than elaborate) sexual signals. *American Naturalist*, 178, 679-686.
- 558 **Caro, S. P., Sewall, K. B., Salvante, K. G. and Sockman, K. W.** 2010. Female Lincoln's
559 sparrows modulate their behavior in response to variation in male song quality. *Behavioral*
560 *Ecology*, 21, 562-569.

- 561 **Cramer, E. R. A. and Price, J. J.** 2007. Red-winged blackbirds *Agelaius phoeniceus* respond
562 differently to song types with different performance levels. *Journal of Avian Biology*, 38,
563 122-127.
- 564 **Darwin, C.** 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- 565 **de Kort, S. R., Eldermire, E. R. B., Cramer, E. R. A. and Vehrencamp, S. L.** 2009. The
566 deterrent effect of bird song in territory defense. *Behavioral Ecology*, 20, 200-206.
- 567 **Derryberry, E. P., Seddon, N., Claramunt, S., Tobias, J. A., Baker, A., Aleixo, A. and**
568 **Brumfield, R. T.** 2012. Correlated evolution of beak morphology and song in the
569 Neotropical woodcreeper radiation. *Evolution*, 66, 2784-2797.
- 570 **Draganoiu, T. I., Nagle, L. and Kreutzer, M.** 2002. Directional female preference for an
571 exaggerated male trait in canary (*Serinus canaria*) song. *Proceedings of the Royal Society*
572 *of London Series B-Biological Sciences*, 269, 2525-2531.
- 573 **DuBois, A. L., Nowicki, S. and Searcy, W. A.** 2011. Discrimination of vocal performance by
574 male swamp sparrows. *Behavioral Ecology and Sociobiology*, 65, 717-726.
- 575 **Fee, M. S., Shraiman, B., Pesaran, B. and Mitra, P. P.** 1998. The role of nonlinear dynamics
576 of the syrinx in the vocalizations of a songbird. *Nature*, 395, 67-71.
- 577 **Forstmeier, W., Kempenaers, B., Meyer, A. and Leisler, B.** 2002. A novel song parameter
578 correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal*
579 *Society of London Series B-Biological Sciences*, 269, 1479-1485.
- 580 **Geberzahn, N. and Aubin, T.** 2014. Assessing vocal performance in complex birdsong: a novel
581 approach. *Bmc Biology*, 12, 9.
- 582 **Goller, F. and Suthers, R. A.** 1996. Role of syringeal muscles in controlling the phonology of
583 bird song. *Journal of Neurophysiology*, 76, 287-300.
- 584 **Goodwin, S. E. and Podos, J.** 2014. Team of rivals: alliance formation in territorial songbirds is
585 predicted by vocal signal structure. *Biology Letters*, 10, 20131083.

- 586 **Hartley, R. S. and Suthers, R. A.** 1989. Airflow and pressure during canary song: evidence for
587 mini-breaths. *Journal of Comparative Physiology A*, 165, 15-26.
- 588 **Hoese, W. J., Podos, J., Boetticher, N. C. and Nowicki, S.** 2000. Vocal tract function in
589 birdsong production: Experimental manipulation of beak movements. *Journal of*
590 *Experimental Biology*, 203, 1845-1855.
- 591 **Huber, S. K. and Podos, J.** 2006. Beak morphology and song features covary in a population
592 of Darwin's finches (*Geospiza fortis*). *Biological Journal of the Linnean Society*, 88, 489-
593 498.
- 594 **Illes, A. E., Hall, M. L. and Vehrencamp, S. L.** 2006. Vocal performance influences male
595 receiver response in the banded wren. *Proceedings of the Royal Society B-Biological*
596 *Sciences*, 273, 1907-1912.
- 597 **Janicke, T., Hahn, S., Ritz, M. S. and Peter, H. U.** 2008. Vocal performance reflects individual
598 quality in a nonpasserine. *Animal Behaviour*, 75, 91-98.
- 599 **Juola, F. A. and Searcy, W. A.** 2011. Vocalizations reveal body condition and are associated
600 with visual display traits in great frigatebirds (*Fregata minor*). *Behavioral Ecology and*
601 *Sociobiology*, 65, 2297-2303.
- 602 **Kunc, H.P., Amrhein, V. and Naguib, M.** 2006. Vocal interactions in nightingales (*Luscinia*
603 *megarhynchos*): more aggressive males have higher pairing success. *Animal Behaviour*,
604 72, 25-30.
- 605 **Lahti, D. C., Moseley, D. L. and Podos, J.** 2011. A tradeoff between performance and
606 accuracy in bird song learning. *Ethology*, 117, 802-811.
- 607 **Lambrechts, M. M.** 1997. Song frequency plasticity and composition of phrase versions in
608 Great Tits *Parus major*. *Ardea*, 85, 99-109.
- 609 **Liu, I. A., Lohr, B., Olsen, B. and Greenberg, R.** 2008. Macrogeographic vocal variation in
610 subspecies of Swamp Sparrow. *Condor*, 110, 102-109.

- 611 **Logue, D. M. and Forstmeier, W.** 2008. Constrained performance in a communication network:
 612 Implications for the function of song-type matching and for the evolution of multiple
 613 ornaments. *American Naturalist*, 172, 34-41.
- 614 **Marler, P. and Peters, S.** 1982. Structural changes in song ontogeny in the Swamp Sparrow
 615 *Melospiza georgiana*. *Auk*, 99, 446-458.
- 616 **Marler, P. and Peters, S.** 1987. A sensitive period for song acquisition in the song sparrow,
 617 *Melospiza melodia* - a case of age-limited learning. *Ethology*, 76, 89-100.
- 618 **Marler, P. and Pickert, R.** 1984. Species-universal microstructure in the learned song of the
 619 Swamp Sparrow (*Melospiza georgiana*). *Animal Behaviour*, 32, 673-689.
- 620 **Moseley, D. L., Lahti, D. C. and Podos, J.** 2013. Responses to song playback vary with the
 621 vocal performance of both signal senders and receivers. *Proceedings of the Royal Society*
 622 *B-Biological Sciences*, 280, 20131401.
- 623 **Mowbray, T.B.** 1997. Swamp sparrow. In: The birds of North American (Poole, A., Gill, F. eds).
 624 Philadelphia: The Academy of Natural Sciences. The American Ornithologists Union: 1-24.
- 625 **Nelson, B. S., Beckers, G. J. L. and Suthers, R. A.** 2005. Vocal tract filtering and sound
 626 radiation in a songbird. *Journal of Experimental Biology*, 208, 297-308.
- 627 **Nowicki, S., Peters, S. and Podos, J.** 1998. Song learning, early nutrition and sexual selection
 628 in songbirds. *American Zoologist*, 38, 179-190.
- 629 **Pasch, B., George, A. S., Campbell, P. and Phelps, S. M.** 2011. Androgen-dependent male
 630 vocal performance influences female preference in Neotropical singing mice. *Animal*
 631 *Behaviour*, 82, 177-183.
- 632 **Petruskova, T., Kinstova, A., Pisvejcova, I., Laguna, J. M., Cortezon, A., Brinke, T. and**
 633 **Petrusek, A.** 2014. Variation in trill characteristics in tree pipit songs: different trills for
 634 different use? *Ethology*, 120, 586-597.
- 635 **Podos, J.** 1996. Motor constraints on vocal development in a songbird. *Animal Behaviour*, 51,
 636 1061-1070.

- 637 **Podos, J.** 1997. A performance constraint on the evolution of trilled vocalizations in a songbird
638 family (Passeriformes:Emberizidae). *Evolution*, 51, 537-551.
- 639 **Podos, J.** 2001. Correlated evolution of morphology and vocal signal structure in Darwin's
640 finches. *Nature*, 409, 185-188.
- 641 **Podos, J., Lahti, D. C. and Moseley, D. L.** 2009. Vocal performance and sensorimotor learning
642 in songbirds. In: *Advances in the Study of Behavior, Vol 40* (Ed. M. Naguib, K. Zuberbuhler,
643 N. S. Clayton and V. M. Janik), pp. 159-195.
- 644 **Podos, J. and Nowicki, S.** 2004. Performance limits on birdsong. In: *Nature's Music: The*
645 *Science of Birdsong* (Ed. P. Marler and H. Slabbekoorn), pp. 318-342. New York:
646 Academic Press.
- 647 **Podos, J., Peters, S. and Nowicki, S.** 2004a. Calibration of song learning targets during vocal
648 ontogeny in swamp sparrows, *Melospiza georgiana*. *Animal Behaviour*, 68, 929-940.
- 649 **Podos, J., Southall, J. A. and Rossi-Santos, M. R.** 2004b. Vocal mechanics in Darwin's
650 finches: correlation of beak gape and song frequency. *Journal of Experimental Biology*,
651 207, 607-619.
- 652 **Poesel, A. and D.A., N.** 2015. Changes in performance of shared and unshared songs within
653 and between years in the white-crowned sparrow. *Ethology*, 121, 850-860.
- 654 **Price, J. J. and Lanyon, S. M.** 2004. Patterns of song evolution and sexual selection in the
655 oropendolas and caciques. *Behavioral Ecology*, 15, 485-497.
- 656 **Reichert, M. S. and Gerhardt, H. C.** 2012. Trade-offs and upper limits to signal performance
657 during close-range vocal competition in gray tree frogs *Hyla versicolor*. *American Naturalist*,
658 180, 425-437.
- 659 **Riede, T. and Goller, F.** 2014. Morphological basis for the evolution of acoustic diversity in
660 oscine songbirds. *Proceedings of the Royal Society B-Biological Sciences*, 281, 20132306.

- 661 **Riede, T., Suthers, R. A., Fletcher, N. H. and Blevins, W. E.** 2006. Songbirds tune their vocal
 662 tract to the fundamental frequency of their song. *Proceedings of the National Academy of*
 663 *Sciences of the United States of America*, 103, 5543-5548.
- 664 **Sakata, J. T. and Vehrencamp, S. L.** 2012. Integrating perspectives on vocal performance and
 665 consistency. *Journal of Experimental Biology*, 215, 201-209.
- 666 **Schmidt, R., Kunc, H. P., Amrhein, V. and Naguib, M.** 2008. Aggressive responses to
 667 broadband trills are related to subsequent pairing success in nightingales. *Behavioral*
 668 *Ecology*, 19, 635-641.
- 669 **Searcy, W. A., Akcay, C., Nowicki, S. and Beecher, M. D.** 2014. Aggressive signaling in song
 670 sparrows and other songbirds. In: *Advances in the Study of Behavior*, Vol 46 (Ed. M.
 671 Naguib, L. Barrett, H. J. Brockmann, S. Healy, J. C. Mitani, T. J. Roper and L. W.
 672 Simmons), pp. 89-125. San Diego: Elsevier Academic Press Inc.
- 673 **Searcy, W. A. and Nowicki, S.** 2005. *The Evolution of Animal Communication: Reliability and*
 674 *Deception in Signaling Systems*. Princeton: Princeton University Press.
- 675 **Seddon, N.** 2005. Ecological adaptation and species recognition drives vocal evolution in
 676 neotropical suboscine birds. *Evolution*, 59, 200-215.
- 677 **Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbuhler, K. and**
 678 **Hammerschmidt, K.** 2010. The central importance of information in studies of animal
 679 communication. *Animal Behaviour*, 80, 3-8.
- 680 **Slabbekoorn, H. and Smith, T. B.** 2000. Does bill size polymorphism affect courtship song
 681 characteristics in the African finch *Pyrenestes ostrinus*? *Biological Journal of the Linnean*
 682 *Society*, 71, 737-753.
- 683 **Sockman, K. W.** 2009. Annual variation in vocal performance and its relationship with bill
 684 morphology in Lincoln's sparrows, *Melospiza lincolnii*. *Animal Behaviour*, 77, 663-671.

- Spencer, K. A. and MacDougall-Shackleton, S. A.** 2011. Indicators of development as sexually selected traits: the developmental stress hypothesis in context. *Behavioral Ecology*, 22, 1-9.
- Suthers, R. A.** 2004. How birds sing and why it matters. In: *Nature's Music: The Science of Birdsong* (Ed. P. Marler and H. Slabbekoorn), pp. 272-295. Amsterdam: Elsevier Academic Press.
- Suthers, R. A., Vallet, E. and Kreutzer, M.** 2012. Bilateral coordination and the motor basis of female preference for sexual signals in canary song. *Journal of Experimental Biology*, 215, 2950-2959.
- Taft, B. N.** 2011. The role of dawn song in tree swallows and its place in the diversity of oscine song learning. PhD thesis, University of Massachusetts, Amherst MA USA.
- Taft, B. N.** 2014. Algorithmic analysis of sounds using morphometric methods. *Journal of the Acoustical Society of America*, 135, 2334.
- Thorpe, W. H. and Lade, B. I.** 1961. The songs of some families of the Passeriformes. II. The songs of the buntings (emberizidae). *Ibis*, 103, 246-259.
- Vehrencamp, S. L., Bradbury, J. W. and Gibson, R. M.** 1989. The energetic cost of display in male sage grouse. *Animal Behaviour*, 38, 885-896.
- Welch, A. M., Semlitsch, R. D. and Gerhardt, H. C.** 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, 280, 1928-1930.
- Westneat, M. W., Long, J. H., Hoese, W. and Nowicki, S.** 1993. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. *Journal of Experimental Biology*, 182, 147-171.
- Wilgers, D. J. and Hebets, E. A.** 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. *Current Zoology*, 57, 175-186.

- 710 **Wilson, D. R., Bitton, P. P., Podos, J. and Mennill, D. J.** 2014. Uneven Sampling and the
711 Analysis of Vocal Performance Constraints. *American Naturalist*, 183, 214-228.
- 712 **Zanollo, V., Griggio, M., Robertson, J. and Kleindorfer, S.** 2013. Males with a faster
713 courtship display have more white spots and higher pairing success in the diamond firetail,
714 *Stagonopleura guttata*. *Ethology*, 119, 344-352.
- 715 **Zollinger, S. A., Podos, J., Nemeth, E., Goller, F. and Brumm, H.** 2012. On the relationship
716 between, and measurement of, amplitude and frequency in birdsong. *Animal*
717 *Behaviour*, 84.
- 718 **Zollinger, S. A. and Suthers, R. A. 2004.** Motor mechanisms of a vocal mimic:
719 implications for birdsong production. *Proceedings of the Royal Society of London*
720 *Series B-Biological Sciences*, 271, 483-491.

721 Table 1. Song type x bird performance scores for our swamp sparrow sample (A=vocal deviation; B=frequency excursion). Descriptive statistics (mean,
 722 standard deviation, and coefficients of variation) are shown in the final 3 columns and rows. Mean CVs are as follows: Vocal deviation x bird, 22.10,
 723 Vocal deviation x song type, 19.19, Frequency excursion x bird, 27.21, Frequency excursion x song type, 16.69.

724

725 A. Vocal deviation:

726

Bird ID

Song Type	1	2	3	4	5	6	7	8	9	10	11	12	means:	stdev:	CV:
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		
means:	2.36	1.81	2.61	2.61	2.31	2.33	2.46	2.88	2.61	2.02	2.84	2.16			
stdev:	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						

727

728 Table 1 continued:

729

730 B. Frequency excursion:

731

Bird ID

Song type	1	2	3	4	5	6	7	8	9	10	11	12	means:	stdev:	CV:
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		

neans: 156.4 201.6 144.0 133.8 141.4 158.7 125.6 112.9 135.8 170.6 179.1 142.2
 stdev: 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

732

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

735 A. Vocal deviation

Factor	Df	SS	F value	<i>p</i> -value
bird	11	3.174	1.191	0.388
song type	11	4.347	1.631	0.215
residuals	11	2.665		

736

737 B. Frequency excursion

Factor	Df	SS	F value	<i>p</i> -value
bird	11	10321	1.931	0.145
song type	11	43586	8.155	<0.001
residuals	11	5345		

738

739 C. Effect sizes

Factor	Eta-sq vocal deviation	Eta-sq frequency excursion
bird	0.302	0.142
song type	0.413	0.597

FIGURE LEGENDS

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 non-trilled organization, Marler & Peters 1987; transitions between trills and note complexes are marked with red 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 seconds, y-axis = 0-10 kHz.

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, recording courtesy of David Logue. The clip is 0.65 s in duration, and the y-axis shown (zoomed in here for illustration purposes) ranges from 2.05 to 8.03 kHz. (B) All points from this 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) The highest amplitude points per time bin, after manual de-selection of candidate highest-amplitude points that the user identified as having captured noise or inter-note intervals rather than actual vocal output; (D) Highest-amplitude points now 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.

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 Figure 1. For song types above the regression lines (e.g., A, C, and 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, and F) fell short of performance levels predicted by vocal deviation alone.

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 is calculated within the sample only, and right panels show data when song sharing is calculated across the population at large. In all cases, song performance declines as the incidence of song sharing increases. The relationship approaches statistical significance for the upper left panel data, and achieves statistical significance for the other three panels (see text). The direction of the observed relationship contradicts our expectation that shared song types would tend to require higher performance.

Figure 5. Frequency excursion values for trilled and non-trilled song sequences from our song sparrow sample. Values shown are medians, 1st and 3rd quartiles, non-outlying minima and maxima, and one - outlier.

Appendix 1: FEX calculator

Appendix 1: FEX Calculator

1 Installation

FEX calculator is freely available and licensed under an open source license. Currently FEX calculator is designed to run on a linux system. Experienced Mac OSX (with X11) users may be able to run it as well, though this is not currently supported. The source code, along with up to date information on building, installing, configuring, and using FEX calculator can be retrieved from <http://behaviorenterprises.com/software.html?pkg=FEX>. After installation you may wish to add a shortcut to the desktop file provided with the program (installed as /usr/share/applications/fex.desktop) in your preferred dock, launcher, menu, or on the desktop.

2 Configuration

FEX calculator can be configured by editing a run-time configuration file in any plain-text editor. A default config-uration file is distributed as /usr/share/fex/config. This file should not be edited; it can be copied to \$XDG_CONFIG_HOME/fex/config or \$HOME/.config/fex/config and edits can be made to the local copy. Read the default configuration file for a complete and up-to-date description of the available options.

2.1 One-time settings

Each laboratory, or each project that uses FEX calculator, should select values for the following options that will be used for all data to be included in the project. Changes in these values can alter the resulting Frequency Excursion values reported, and sometimes substantially so.

bandpass bandpass filter applied to audio before any processing is done. The values are for the low and high cutoffs in KHz.

threshold value — in decibels below the peak amplitude of the recording — below which points will be excluded from the analysis. Points above this cutoff are only *candidates* for inclusion in the analysis and will be included if the point is the highest amplitude of the points remaining in the time bin after extraneous points have been *erased*.

samples number of samples per time bin for the FFT. It is recommended to set this relative to the sample rate of the audio recordings: for 44.1 KHz audio use 256; for 22.05 KHz use 128. More generally, this should be the sample rate (in KHz) times 5.805.

2.2 Adjustable settings

The following settings can be adjusted at any time as desired. These settings will allow each user to customize the interface to their liking. Changes to these settings will not affect the calculation of Frequency Excursion values. The colors and fonts of various elements of the user interface can also be specified in the configuration file. Details on color and font settings can be found in the default configuration file.

window windowing function for the fft. This can be set to any of the following: hanning, hamming, blackman, nutall, blackman-nutall, blackman-harris, rectangular, or custom. If 'custom' is specified

it can be followed by up to 4 floating point numbers specifying the coefficients for a generalized cosine windowing function.

floor sound floor for the spectrogram display, in dB below the maximum amplitude. Higher values are more inclusive and will produce a darker background spectrogram.

scale number of graphical units per data unit. Higher values will provide a greater visual resolution making it easier to differentiate separate points. Higher values will, however, also use more system memory.

help command executed to display the online help window — this should likely only be changed to select the default terminal emulator if xterm is not installed.

color colors for the interface are specified with five floating point values from 0.00 to 1.00 specifying the red, green, and blue components of the color followed by the alpha (opacity) level and a width/size parameter.

3 Usage

3.1 Overview

The *FEX calculator* package contains two executable files: the compiled binary **fex** and a python script front-end **fex-gtk**. In most cases, only **fex-gtk** should be used directly. Details of **FEX calculator** are provided in the manual page distributed with the software.

Fex-gtk is a front-end of the program that facilitates batch processing of large numbers of wave files. **Fex-gtk** can be provided a list of file names, or can be run with no parameters to trigger a dialog window to select wave files. **FEX calculator** will be run on each input file, and the results can either be stored to a data file or displayed in a dialog window upon completion.

Fex-gtk is also the executable target of **fex.desktop** which is distributed with *Fex*. **fex.desktop** allows for drag-and-drop operation of *Fex*. The desktop file can accept any number of wave files as a drop target.

3.2 Starting FEX calculator

Assuming a shortcut to **fex.desktop** has been added to the desktop or your preferred launcher/dock, you can drag any number of wave files from your file manager and drop them on the icon. FEX calculator will process one file at a time.

3.3 Analysis: step-by-step

The steps below outline a recommended approach to analysing a song in *FEX calculator*. The key binding or controls for each step are listed as bullet points under that step. Many controls specify a direction which can be indicated with the keyboard arrow keys, home-row directional keys (h, j, k, l), or with a 2-axis mouse scroll-wheel. Many controls also specify a modifier key to be held down with the key or directional indicator. Press 'F1' at any time in Fex to open a help window outlining these and other controls.

1. **Crop** out the region of interest. Everything outside of the selected region will be ignored for the remainder of the calculation. Use this function to select the elements of interest: a set of repeated syllables, a note, or a full song.

- 'c' or "crop" button on the tool window
- right-click on the "crop" button to return to the original full signal

2. Optionally adjust the **floor** value as desired. This will only affect the display of the background spectrogram.
 - Control+Shift+Left for darker spectrogram
 - Control+Shift+Right for lighter spectrogram
3. Adjust the **threshold** if needed. *Caution:* this will affect the calculation of frequency excursion as it will make the calculation more or less inclusive. Most projects should select a standard threshold that will be held constant across all audio samples analyzed.
 - Control+Shift+Up for a higher more-exclusive threshold
 - Control+Shift+Down for a lower threshold
4. **Erase** extraneous points and/or noise. Any of the following may aid in differentiating signal from noise and may be used as needed in any order to clean up the signal.
 - (a) **Zoom** in as needed.
 - Control+Up or Control+Down to zoom in/out
 - Up, Down, Left, or Right to pan while zoomed in
 - (b) **Toggle** visibility of the points and lines overlay to view the regular spectrogram.
 - 't' to toggle
 - (c) **Play** the signal. Note that this plays only what is in the current view. If you have zoomed in this will not play the full signal being analyzed, but only the portion zoomed in to.
 - 'p' to play
 - Shift, Control, or Alt and 'p' to play at slower speeds
 - (d) Adjust **point** or **line** sizes.
 - Shift+Up or Shift+Down for larger/smaller points
 - Shift+Left or Shift+Right for thinner/wider lines
 - (e) **Erase**. Pay particular attention to reverberation between syllables, harmonics above the signal, and any low-frequency noise not removed by the bandpass filter.
 - 'e' or "Erase" button on the tool window toggle to the eraser
 - Alt+Up or Alt+Down for a larger/smaller eraser
 - Alt+Left or Alt+Right for a taller/wider eraser
 - Once in erase mode, the left mouse button will remove any points under the eraser cursor. You can drag while holding the mouse button to erase an area
 - (f) If you unintentionally erase, you can **undo** up to 7 steps.
 - 'u' to undo
5. **Zoom out** for a full overview and **adjust** points and lines to ensure nothing was missed. Sometimes a stray point (often from a harmonic) might be easy to miss — substantially larger/heavier points and lines will make such points stand out.
 - Control+Down to zoom all the way out
 - Shift+Up or Shift+Down for larger/smaller points
 - Shift+Left or Shift+Right for thinner/wider lines
6. **Exit**, the frequency excursion value displayed in the tool-window when the program exits will be recorded and optionally saved to a data file (see next section). You may also discard the value for the current signal and output an 'NA' instead — this is useful if you determine the recording was not of sufficient quality to get an accurate measure.

- Control+q to exit normally saving the value
- Control+Shift+q to exit and discard the value (output an 'NA')

3.4 Saving data

If you selected multiple wave files for analysis (dropped multiple files on the icon, or selected multiple files from the file dialog) FEX calculator will prompt you to save the results as a tab-separated data sheet which can be imported into any data analysis program. If you selected only a single file, the resulting frequency excursion value will be displayed in a dialog box and will not be recorded in any data file.

4 Code excerpts

4.1 Fourier Transformation

4.1.1 Data Structures

The data structure for the Fourier transformation is defined in *fex.h* as shown below. The **freq** and **time** variables are arrays of length **nfreq** and **ntime** respectively. These arrays store the frequency in Hz of each frequency step and the time in seconds of each time bin. The two dimensional array **amp** stores the amplitude values in decibels relative to the signal peak for each time-frequency point. The simple variables **max** and **min** store the highest and lowest amplitude values for the full signal. The final two dimensional array **mask** records which points in **amp** have been erased (each time-frequency point is represented by an 8-bit mask allowing for up to 8 undo-levels in erasing).

```
typedef struct FFT {
    double **amp;
    double *time;
    double *freq;
    double max, min;
    int nfreq, ntime;
    char **mask;
} FFT;
```

This **FFT** data structure is filled via the **create_fft** function in *fft.c* as described below. First, memory is allocated for each of the data elements. The number of frequency bins (the frequency resolution) is directly dependent on the window length of the Fourier transformation as selected in the configuration file. The number of time bins depends on the number of samples in the audio file (the sample rate times the duration) and the configured hop size.

```
#define FFTW_FLAGS FFTW_FORWARD, FFTW_ESTIMATE
FFT *create_fft(Wave *wav) {
    /* allocate memory */
    FFT *fft = (FFT *) calloc(1, sizeof(FFT));
    fft->nfreq = conf.winlen/2 + 1;
    fft->ntime = wav->samples/conf.hop;
    fft->amp = (double **) calloc(fft->ntime, sizeof(double *));
    fft->time = (double *) calloc(fft->ntime, sizeof(double));
    fft->freq = (double *) calloc(fft->nfreq, sizeof(double));
    fft->mask = (char **) calloc(fft->ntime, sizeof(char *));
}
```

Next, the Nyquist frequency is calculated from the sample rate, and the step sizes for the **freq** and **time** arrays are calculated. These step sizes are used to fill the arrays.

```
/* calculate step sizes and fill time/freq arrays */
double nyquist = (double) wav->rate / 2000.0;
double df = nyquist / fft->nfreq;
double dt = (double)wav->samples / (double)(wav->rate * fft->ntime);
```

```

1014     double f, t;
1015     int i, j;
1016     for (i = 0, f = 0.0; i < fft->nfreq; i++, f += df) fft->freq[i] = f;
1017     for (i = 0, t = 0.0; i < fft->ntime; i++, t += dt) fft->time[i] = t;
1018
1019
1020
1021

```

4.1.2 Calculation

The `create_fft` function next prepares the data for a call to the `fftw` library by allocating memory for the input and output data structures for `fftw`. In order to properly window the **FFT** data for `fftw` a multiplier array is filled based on the selected windowing function. Any 4-parameter cosine function can be used — the default is a *hanning* window with the values 0.5, 0.5, 0, 0.

```

1029     /* prepare fftw */
1030     fftw_complex *in, *out;
1031     fftw_plan p;
1032     in = (fftw_complex *)fftw_malloc(conf.winlen * sizeof(fftw_complex));
1033     out = (fftw_complex *)fftw_malloc(conf.winlen * sizeof(fftw_complex));
1034     p = fftw_plan_dft_1d(conf.winlen, in, out, FFTW_FLAGS);
1035     /* create windowing function */
1036     double window[conf.winlen];
1037     double *a = conf.win->a;
1038     double wl = conf.winlen;
1039     for (i = 0; i < conf.winlen; i++)
1040         window[i] = a[0] - a[1] * cos(2 * M_PI * (i / (wl - 1.0))) +
1041                     a[2] * cos(2 * M_PI * (i / (wl - 1.0))) -
1042                     a[3] * cos(2 * M_PI * (i / (wl - 1.0)));
1043

```

Calculation continues by looping over all the time bins and first allocating memory for the amplitudes (and mask values) for each time bin. The windowing function created above is used to copy a block of the signal data into the input for `fftw`. This windowed data is passed to `fftw` and the results are stored in one column of the amplitude matrix (as the absolute values of the complex-valued result).

```

1049     /* loop over signal */
1050     int pos;
1051     for (pos = 0, j = 0; pos < wav->samples; pos += conf.hop, j++) {
1052         fft->amp[j] = (double *) malloc(fft->nfreq * sizeof(double));
1053         fft->mask[j] = (char *) calloc(fft->nfreq, sizeof(char));
1054         /* copy windowed chunk to data */
1055         for (i = 0; i < conf.winlen; i++) {
1056             if (pos + i < wav->samples) {
1057                 in[i][0] = wav->d[pos + i] * window[i];
1058                 in[i][1] = 0.0;
1059             }
1060             else {
1061                 in[i][0] = 0.0;
1062                 in[i][1] = 0.0;
1063                 goto doublebreak;
1064             }
1065         }
1066         /* calculate fft & fill amp matrix */
1067         fftw_execute(p);
1068         for (i = 0; i < fft->nfreq; i++)
1069             fft->amp[j][i] = sqrt(out[i][0] * out[i][0] +
1070                                 out[i][1] * out[i][1]);
1071     }
1072

```

After all time bins have been processed, any remaining time bins are zeroed out. Any values outside the hi and low pass filter settings are also zeroed out.

```

80 doublebreak:
81     fftw_destroy_plan(p);
82     fftw_free(out);
83     fftw_free(in);
84     /* fill and zero unused bins */
85     for ( ; j < fft->ntime; j++) {
86         fft->amp[j] = (double *) calloc(fft->nfreq, sizeof(double));
87         fft->mask[j] = (char *) calloc(fft->nfreq, sizeof(char));
88     }
89     /* band pass filter */
90     for (i = 0; i < fft->ntime; i++) {
91         for (j = 0; j < fft->nfreq && fft->freq[j] < conf.hipass; j++)
92             fft->amp[i][j] = 0;
93         for (j = fft->nfreq - 1; j > conf.lopass; j--)
94             fft->amp[i][j] = 0;
95     }

```

Finally, the maximum amplitude is found, then all amplitude values are divided by this maximum and converted to decibels. The maximum (always zero) and minimum amplitudes relative to the peak are stored for later use in the spectrogram creation.

```

96     /* normalize, log transform, and scale to dB */
97     fft->max = fft->min = 0.0;
98     for (i = 0; i < fft->ntime; i++) for (j = 0; j < fft->nfreq; j++)
99         if (fft->amp[i][j] > fft->max) fft->max = fft->amp[i][j];
100     for (i = 0; i < fft->ntime; i++) for (j = 0; j < fft->nfreq; j++) {
101         fft->amp[i][j] = 10.0 * log10(fft->amp[i][j] / fft->max);
102         if (fft->amp[i][j] < fft->min && fft->amp[i][j] > -900)
103             fft->min = fft->amp[i][j];
104     }
105     fft->max = 0.0;
106     return fft;
107 }

```

4.2 Frequency Excursion Calculation

4.2.1 Data Structures

The data structure for the frequency excursion calculation is defined in the **Spectro** structure in *fex.h* as shown below. Several variables in this structure store spectrogram image data, as well as the points and lines overlays. Most relevant to the calculation are the variables **pex**, the path length of the lines, **text**, the time span of the lines, and **fex** which is the path length divided by the time span.

```

1122 typedef struct Spectro {
1123     const char *fname;
1124     char *name;
1125     unsigned char *a_spec, *a_thresh;
1126     cairo_surface_t *m_spec, *m_thresh, *s_points;
1127     FFT *fft;
1128     int fft_x, fft_y, fft_w, fft_h, fft_lo, fft_hi;
1129     double pex, tex, fex;
1130 } Spectro;

```

This **Spectro** data structure is filled via the **spectro_points** function in *spectro.c* as described below. First, previous image data elements are reset as needed, then local variables **lt** and **lf** (representing “last” or previous time and “last” or previous frequency) are set to the first time bin and first frequency value at the start of the signal. Next **pex** and **tex** are zeroed.

```

1136
1137
1138
1139
1140
1141
1142
1143
1144
1145
1146
1147
1148
1149
1150
1151
1152
1153
1154
1155
1156
1157
1158
1159
1160
1161
1162

126 int spectro_points() {
    if (spect->s_points) cairo_surface_destroy(spect->s_points);
128   spect->s_points = cairo_image_surface_create(CAIRO_FORMAT_ARGB32,
        spect->fft_w * conf.scale, spect->fft_h * conf.scale);
130   cairo_t *p = cairo_create(spect->s_points);
    cairo_t *l = cairo_create(spect->s_points);
132   set_color(p,RGBA_POINTS);
    set_color(l,RGBA_LINES);
134   int i, j, f;
    double lt = spect->fft->time[0], lf = spect->fft->freq[0];
136   spect->pex = 0.0;
    spect->tex = 0.0;

```

4.2.2 Calculation

The **spectro_points** function continues by looping through every time bin in the signal. In each time bin, point with the maximum amplitude that has not been erased (i.e. masked) is found. If this point is above the minimum threshold selected, this point is added to the calculation by finding the distance from the coordinate **lt**, **lf** to the current point's time-frequency coordinate. **lt** and **lf** are then set to this current point to be the starting point of the next line segment. Lastly, the cumulative **pex** value is divided by the cumulative **tex** value to get the **fex** or frequency excursion value. Function calls starting with **cairo_** are graphics functions for recreative the visual display but do not contribute to the calculation of frequency excursion.

```

1163  /* loop through time bins */
1164  for (i = spect->fft-x; i < spect->fft-w + spect->fft-x; i++) {
1165
1166      /* find maximum (non masked) frequency in time bin */
1167      for (f = 0, j = spect->fft-y; j < spect->fft-h+spect->fft-y; j++) {
1168          if (spect->fft->mask[i][j]) continue;
1169          if (spect->fft->amp[i][j] > spect->fft->amp[i][f] || !f)
1170              f = j;
1171      }
1172      /* add points and do calculations if f is above threshold */
1173      if (f > 0 && spect->fft->amp[i][f] > conf.thresh) {
1174          if (!t == spect->fft->time[0]) {
1175              spect->pex += sqrt(
1176                  (spect->fft->freq[f] - lf) * (spect->fft->freq[f] - lf) +
1177                  (spect->fft->time[i] - lt) * (spect->fft->time[i] - lt) );
1178              spect->tex += spect->fft->time[i] - lt;
1179          }
1180          lt = spect->fft->time[i];
1181          lf = spect->fft->freq[f];
1182          cairo_line_to(l,
1183                      (i - spect->fft-x) * conf.scale + conf.scale / 2,
1184                      (f - spect->fft-y) * conf.scale + conf.scale / 2);
1185          cairo_new_sub_path(p);
1186          cairo_arc(p,
1187                  (i - spect->fft-x) * conf.scale + conf.scale / 2,
1188                  (f - spect->fft-y) * conf.scale + conf.scale / 2,
1189                  conf.col[RGBA_POINTS].w, 0, 2*M_PI);
1190      }
1191      spect->fex = spect->pex / spect->tex;
1192  }
1193  cairo_fill(p);
1194  cairo_stroke(l);
1195  cairo_destroy(p);
1196  cairo_destroy(l);
1197  return 0;
1198  }

```

1199

Figure 1 rev

Frequency

Time

Figure 2

A

B

C

D

Figure 3

Figure 4

Figure 5