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

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1	A Fine-Scale, Broadly-Applicable Index of Vocal Performance:
2	Frequency Excursion
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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 deviation, is limited by being applicable only to vocal trills, and also overlooks certain 25 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 neighbors. In song sparrows, frequency excursion values of trilled song segments 36 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

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

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44 INTRODUCTION

45 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 46 prospective mates (Andersson 1994; Searcy & Nowicki 2005; Seyfarth et al. 2010; 47 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 vocal tract (reviewed by Suthers 2004; Podos & Nowicki 2004; Podos et al. 2009; Riede 62 63 & Goller 2014). Performance challenges arise as birds coordinate syrinx modulations 64 with intricately patterned respiratory movements, and as they track changing source frequencies via precise reconfigurations of the vocal tract (Westneat et al. 1993; Hoese 65

et al. 2000; Podos et al. 2004b; Riede et al. 2006; Suthers et al. 2012). Studies of handreared 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 77 78 correspondingly rapid and extensive modulations of components of the vocal apparatus 79 (Podos et al. 2009). Moreover, trill rate and frequency bandwidth should relate to each 80 other inversely, because of an expected tradeoff at maximal performance between rates 81 and spans of vocal modulations. An initial structural analysis of trilled song sequences 82 of 34 species of emberizid songbirds supported this expectation: songs in a family-wide 83 trill rate by frequency bandwidth plot show a lower-left skewed triangular distribution, 84 with some trills showing fast trill rates or broad frequency bandwidths but not both 85 concurrently (Podos 1997). Similar triangular distributions have since been reported for diverse taxa including numerous avian and one mammalian species (e.g., Price & 86 87 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).

91 Descriptions of trill rate and frequency bandwidth, and of tradeoffs between the two, not 92 only help describe constraints on trill production but have also provided a means to test 93 the functional relevance of trill performance variations. Trill rate and frequency 94 bandwidth are in themselves useful measures of vocal performance. Moreover, as a 95 composite index of performance for any trill, one can graph a trill sequence of interest 96 on a taxon-wide plot of trill rate by frequency bandwidth, and calculate the offset 97 between the trill in question and the putative performance constraint. Operationally this 98 calculation involves the derivation of a trill rate by frequency bandwidth "upper-bound 99 regression" (Podos 1997), and calculation of the orthogonal distance between the upper 100 bound regression and the trill of interest (Podos 2001; Ballentine et al. 2004). The 101 resulting distance, termed "vocal deviation", corresponds inversely to presumed vocal 102 performance requirements: higher vocal deviations are indicative of low performance 103 songs, and vice versa. Vocal deviation, trill rate, and frequency bandwidth have now 104 been calculated in a diverse array of studies, and shown in some cases to correlate with 105 beak dimensions (Podos 2001; Huber & Podos 2006; Ballentine 2006; Sockman 2009; 106 Derryberry et al. 2012), body mass and age (Ballentine 2009), the vigor of solicitation 107 displays or strength of spatial preference by females (Ballentine et al. 2004; Caro et al. 108 2010; see also Draganoiu et al. 2002), the strength and direction of song playback 109 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).

112 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 113 114 aspects of vocal structure that may impact performance and thus hold signal value. In 115 particular, vocal deviation cannot account for frequency and temporal variations within 116 syllables, beyond calculated differences between minimum and maximum frequencies. 117 These variations include numbers and sequences of notes within syllables, rates and 118 patterns of frequency modulation within notes, and relationships between ending and 119 starting frequencies of sequential notes (e.g., Podos et al. 2009, their Fig. 1: see also 120 Geberzahn & Aubin 2014). In all of these parameters, the production of syllables or 121 syllable sequences with gradually or steadily shifting frequencies should entail less 122 vigorous motor activity than the production of syllables or syllable sequences with rapid 123 or numerous frequency shifts or reversals. A second main limitation of the vocal 124 deviation index is that it can be applied only to trilled sequences (Geberzahn & Aubin 125 2014; Cardoso 2014). While many species trill, others do not and at present we have no 126 clear guideline for guantifying non-trilled song performances, or for comparing 127 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

133 calculated in two steps, as described in more detail in the methods section below. First, 134 for each vocal segment of interest, we calculate peak frequencies in successive time 135 bins, thus characterizing the segment's frequency contours. Second, we sum 136 spectrogram "distances" between successive time by frequency points across the entire 137 sample, including across inter-note and inter-syllable intervals, and standardize this 138 summed distance to a per-second basis. Frequency excursion thus provides a 139 cumulative assessment of frequency modulation rates across the course of an entire 140 song or song segment. As in Gerberzahn & Aubin (2014), frequency excursion accounts 141 for the vocal performance assumed to occur during silent intervals between notes, 142 following the assumption that reconfigurations of the vocal apparatus are more 143 extensive when note transitions involve larger frequency jumps (see also Westneat et 144 al. 1993; Podos et al. 2004b; Cardoso 2014). Higher frequency excursion values 145 should correspond to more active, rapid, or extensive vocal activity (i.e., more 146 pronounced reconfigurations of the vocal apparatus per unit time), and thus indicate 147 greater required vocal performance.

148 Along with this report we are making available a program one of us (JM) has written to 149 facilitate the measurement of frequency excursion (Appendix 1). We also present 150 sample applications focusing on three diverse questions about vocal performance in 151 three songbird species (Fig. 1): chipping sparrows (Spizella passerina), swamp 152 sparrows (Melospiza georgiana), and song sparrows (Melospiza melodia). First, for all 153 three species we calculate correlations between vocal deviation and frequency 154 excursion, and ask how songs' distributions on regression plots correspond to their 155 spectrographic structure. Following the logic presented above, we expect that frequency

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156 excursion will provide a more precise accounting of within-syllable vocal performance, 157 as inferred from spectrograms and based on assumptions about vocal mechanics. We 158 next ask, within our swamp sparrow sample, the following question: for a species with 159 song repertoires and a population that shares song types, how does song performance 160 vary within individuals versus within song types (across individuals)? As first noted by 161 Cardoso et al. (2009, see also 2012), birds with song repertoires likely vary in 162 performance levels across their song types, whereas song types that are shared among 163 birds likely attain similar performance levels across the population. As with dark-eved 164 juncos (Junco hyemalis), we expect that performance variation within the repertoires of 165 individual swamp sparrows will exceed performance variation within shared song types 166 (Cardoso et al. 2009). In our swamp sparrow sample we also compare performance 167 levels of shared versus unshared song types. We predict that the vocal performance of 168 shared song types will exceed that of unshared song types, following the hypothesis 169 that shared song types provide a means for comparing multiple singers and thus might 170 be subject to enhanced sexual selection pressures (Logue & Forstmeier 2008). 171 Consistent with this prediction, Poesel & Nelson (2015) have shown that vocal 172 performance (sensu Forstmeier et al. 2002) is higher for shared than unshared song 173 types in Puget Sound white-crowned sparrows (Zonotrichia leucophrys pugetensis). 174 Finally we ask, within our song sparrow sample, whether performance levels in trilled 175 song sequences exceed those in non-trilled song sequences. This test is possible in 176 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 177 178 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.

185 METHODS

186 Song sample

187 Songs of swamp and song sparrows used in this analysis were recorded from banded 188 populations in Western Massachusetts (Hampshire and Franklin County MA). Chipping 189 sparrow songs were obtained from the same region from both banded and un-banded 190 populations, with supplementary recordings obtained from the Macaulay Library at the 191 Cornell Lab of Ornithology. Field recordings were made using Marantz PMD660 digital 192 recorders (sample rate 44.1 kHz) and Sennheiser directional microphones (ME66) or 193 omnidirectional microphones (ME62) mounted in Telinga parabolas. Some of these 194 recordings were obtained in prior studies (Lahti et al. 2011, Moseley et al. 2013, 195 Goodwin & Podos 2014). Swamp sparrow and chipping sparrow songs are comprised 196 of single trills; song sparrow songs include trills interspersed with note complexes 197 (Marler & Peters 1987; illustrated in Fig. 1). For each song sparrow song, we chose the 198 longest-duration trill and the longest-duration note-complex within each song for 199 analysis. Some song sparrow trills start at a slow pace; in such cases, we only 200 measured in our analyses the final, temporally-consistent segment of the trill (e.g., Fig.

201 1E opening trill, final 3 syllables only). The three focal species vary in song type 202 repertoire sizes: individual chipping sparrows sing only a single song type; swamp 203 sparrows sing between 2 and 5 song types, and song sparrows sing about 12 to 15 204 song types. Our sample size was as follows: chipping sparrows, 54 birds, 54 song 205 types; swamp sparrows, 12 birds, 34 song types; song sparrows, 6 birds, 13 song 206 types. This listing of song type sample size does not consider whether song types were 207 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. 208 209 Performance values measured from multiple renditions per bird of the same song type 210 were averaged prior to further statistical assessment.

211 Calculating vocal deviation

212 Vocal deviations from swamp and chipping sparrow songs, and from trilled segments of 213 song sparrow songs, were calculated using established methods (Podos 1997, 2001; 214 Huber & Podos 2006; Moseley et al. 2013). In brief, for each trill type from each bird, we 215 calculated, using SIGNAL 4.0 (Beeman 2002), two parameters: (1) trill rate (Hz) as the 216 number of syllables produced per second, measured from waveforms and spectrograms 217 using an on-screen cursor; and (2) frequency bandwidth (kHz) i.e., the difference 218 between maximum and minimum frequencies, as measured from amplitude spectra at -219 24 dB relative to the trill's peak amplitude (illustrated in Podos 1997, see also Zollinger 220 et al. 2012). We then calculated the orthogonal distance of each trill to two family-wide 221 upper-bound regressions of trill rate (Hz) by frequency bandwidth (kHz). The first of 222 these upper-bound regressions was calculated using a standard method, in which

223 sample data were parsed into x-axis bins of equal width, and maximal values per bin 224 used for the regression calculation (y = -0.124x + 7.55, Podos 1997). The second 225 upper-bound regression was calculated using a 90% guantile regression method, which 226 aims to avoid biases associated with skewed sample distributions (G. Beckers, C. ten 227 Cate, & E. Meelis pers. comm., Wilson et al. 2014; y = -0.089x + 5.96 for the data set 228 from Podos 1997). Results from analyses using both upper-bound regressions were 229 highly similar, as indicated in several ways including very strong correlations between vocal deviation values calculated by the standard and quantile methods (chipping 230 231 sparrows, r=0.977; swamp sparrows, r=0.996, song sparrows, r=-0.995; all P < 0.001). 232 For the remainder of the paper we report vocal deviation data based only on the first 233 method.

234

235 Calculating frequency excursion

236 Frequency excursion ("FEX") was calculated using an original open-source Linux 237 program, "FEX calculator" (see Appendix 1 for program code, operational notes, and 238 program website). FEX calculator queries users for three input parameters: (1) 239 frequency filter values (to filter out extraneous noise above or below those of interest); 240 (2) the selected amplitude threshold value (dB below peak threshold), below which 241 sound energy in each clip is excluded in peak frequency calculations; and (3) fft sample 242 size (# of samples per time bin). For all of our analyses here, we applied a frequency 243 filter to exclude input below 1.25 kHz or above 10 kHz, an amplitude threshold value of -244 24 dB relative to the segment's peak frequency (the same threshold used for our vocal

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245 deviation calculations), and an fft value of 256 points (which allows a frequency 246 resolution of 0.172 kHz for audio clips with a standard 44.1 kHz sample rate). Applied to 247 an input sound clip, FEX calculator generates a spectrogram (Fig. 2A) indicating all 248 points above the dB threshold (Fig. 2B) with peak frequency value points overlaid (Fig. 249 2C). While most of these points map cleanly onto song notes, others appear in the 250 intervening silences between notes, or occasionally correspond to background sounds 251 or noise. FEX calculator allows users to zoom in and delete "false" bin points as 252 assessed by eye, i.e. points that appear to correspond to background noise or other 253 sources besides the focal signal. FEX calculator then calculates and sums the linear 254 distances, on the spectrogram, between temporally adjacent points including those that 255 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 256 257 were calculated only for 6 syllables within (the middle portions of) chipping sparrow and 258 swamp sparrow trills, and calculated across the full temporally-stable duration of song 259 sparrow trills.

260 <u>Question 1: How do frequency excursion and vocal deviation compare as measures of</u> 261 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

267	deviation values (i.e., shorter distances from the upper-bound maxima) and higher
268	frequency excursion values. Next, in a qualitative exercise, we plotted frequency
269	excursion as a function of vocal deviation, overlaid linear regressions, and then
270	assessed the position of sample points relative to the regression line. We expected that
271	position on these plots relative to the regression line would correspond to a trill's fine-
272	scale phonological structure, especially in terms of the extent and/or rapidity of fine-
273	scale frequency modulations. In particular we expected that trills with the abrupt and
274	rapid modulations (within-notes) and transitions (between notes) – both attributes
275	invisible to vocal deviation would be positioned above the regression line, whereas
276	trills with relatively smooth frequency modulations and transitions would appear below
277	the regression line.
278	Question 2: For repertoire species, what are the relationships between vocal
279	performance and song type sharing?
280	This analysis focused on swamp sparrows, which in our sample featured some song
281	types that were shared by two or more birds (with sharing determined by visual
282	assessment of spectrograms). We calculated, for each song type sung by each bird, our
283	two indices of vocal performance. Next, for each bird and song type, we calculated
284	index means, standard errors, and coefficients of variation (CV).
285	We then assessed, via ANOVA, the relative contributions of song type versus bird (i.e.,
286	within-individual versus between-individual factors) to variation in each metric of vocal
287	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.

298 <u>Question 3: How does vocal performance vary in trilled versus non-trilled song</u> 299 <u>sequences?</u>

300 This analysis focused on our song sparrow sample, a species whose songs contain 301 both trilled and non-trilled song sequences. For each song analyzed we calculated 302 frequency excursion from one note complex and one trilled sequence. There were a 303 number of decisions we had to make when calculating frequency excursion for note-304 complexes. First, we only focused on segments of note complexes that appeared in 305 multiple renditions of songs. This was necessary given that song sparrows regularly 306 omit some segments from their note complexes across multiple renditions of a given 307 type (Podos et al. 1992). Second, when perusing of song sparrow songs for these 308 analyses, we noted an unexpectedly large proportion of songs that featured double-309 voicing, in which two fundamental frequencies are voiced simultaneously. While this is a

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310 potentially important aspect of vocal performance, our frequency excursion metric is not 311 able to account for this axis of performance, given that calculating frequency excursion 312 requires selection of a single peak frequency per time bin. We thus excluded songs 313 without double-voicing from our sample. Third, we opted to omit buzzes in our note 314 complex frequency excursion calculations. Most note complexes include buzzes, 315 defined as having amplitude modulation rates of 35 Hz or greater, and being produced 316 via pulsatile rather than mini-breath respiration (e.g., Hartley & Suthers 1989). For each 317 note complex with one or more buzzes, we calculated frequency excursion for all song 318 segments before, after, and between buzzes, and then generated a composite 319 frequency excursion value for each note complex as the sum of all resulting path 320 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.

325

326 RESULTS

327 Frequency excursion versus vocal deviation

328 The three species examined here differed widely in vocal deviation, with chipping

329 sparrows achieving the highest performance (mean ± SD vocal deviation scores = 1.54

 \pm 0.76), followed by swamp sparrows (2.43 ± 0.58) and then by song sparrows (3.42 ±

331	1.26; ANOVA $F_{2,12}$ = 35.26, $P < 0.001$, all Tukey HSD $P < 0.001$). By contrast, as
332	measured by frequency excursion, chipping and swamp sparrows achieved roughly the
333	same vocal performance levels, while song sparrows retained their lowest-performance
334	rank (chipping sparrows 146.0 \pm 42.8; swamp sparrows 149.4 \pm 47.0; song sparrows
335	83.0 ± 30.5; ANOVA $F_{2,12}$ = 12.73, P < 0.001, Tukey HSD for chipping x song sparrow
336	and swamp x song sparrow P < 0.001, Tukey HSD for chipping x song sparrow P >0.5).
337	For all three species, our two vocal performance indices correlated negatively with each
338	other, as expected (chipping sparrows, r=-0.64, p<0.001; swamp sparrows, r=-0.60,
339	p<0.001; song sparrows, r=-0.65, p=0.016). The strength of the correlation in swamp
340	sparrows is lessened yet retains statistical significance when we remove one notable
341	high-performance outlier (r=-0.43, p=0.012). In Figure 3 we present plots comparing
342	values generated by the two performance indices. Songs on this plot above the
343	regression lines tend to have features that we presume require high vocal performance.
344	Such features include rapid frequency modulations and large frequency jumps between
345	the end and start of successive notes (e.g., Figure 1A, C). By contrast, songs below the
346	regression lines tended to show more gradual frequency modulations both within and
347	between notes (e.g., Figure 1B, D).

348 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

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352 analyzed (birds and song types). This is shown in our results in two ways. First, an 353 ANOVA based on vocal deviation (Table 2A) failed to identify significant contributions by 354 either factor to sample-wide vocal performance variation, whereas an ANOVA based on 355 frequency excursion (Table 2B) revealed significant contributions of song type. Second, 356 inspection of effect sizes suggests that song type is a greater contributor than individual 357 bird to the overall sample variation in performance, with this difference being more 358 pronounced for frequency excursion (Table 2C). These outcomes are consistent with 359 the expectation that song types are more important than individual birds in defining a 360 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 withintypes 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* 374 = 0.013). When we measured song sharing across the population at large (Fig. 4 right
 375 panels), the relationship achieved statistical significance with both performance indices

376 (vocal deviation: $r_s = 0.465$, $F_{1,11} = 119.88$, P = 0.048; frequency excursion: $r_s = -0.508$,

377 $F_{1,11} = 455.19, P = 0.043$).

378 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 ttest, df=11, t=1.131, p=0.282).

384

385 DISCUSSION

386 Our two main goals in this paper were to introduce the frequency excursion index, and 387 to apply it to representative questions about vocal performance. A key attribute of our 388 frequency excursion index is that it characterizes not just frequency modulations within 389 notes, but also frequency transitions between notes, i.e. during the silent gaps in song. 390 As such, frequency excursion builds on the suggestion of Podos et al. (2009, their 391 Figure 1) and parallels a method developed by Geberzahn & Aubin (2014) to quantify 392 vocal performance in skylarks (*Alauda arvensis*). While we here apply the frequency 393 excursion method to songbird songs, we note that it could be applied readily to other 394 taxa and vocalizations of interest.

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395 Before discussing our data and analyses it is worth emphasizing that frequency 396 excursion is not suited to capture all potentially significant aspects of vocal 397 performance. A first such example concerns modulations in amplitude, with broader 398 amplitude modulations or the ability to sing at consistently high amplitudes likely 399 indicating higher vocal performance (Forstmeier et al. 2002). Frequency excursion also 400 cannot be applied to the analysis of non-tonal sounds, in which peak frequencies cannot 401 be identified with confidence within each time bin. It thus cannot be applied readily to 402 analysis of buzzes, harmonic stacks, two-voiced sounds, or other complex vocal 403 phenomena that all likely challenge singers' performance limits (e.g., Fee et al. 1998). 404 The frequency excursion index also contains, in its construction, at least four implicit 405 assumptions about vocal mechanics: (i) more extensive frequency modulations both 406 within and between notes require higher levels of performance; (ii) frequency 407 modulations within and between notes can be scaled for performance equivalently. 408 using identical frequency by time parameters; (iii) frequency up-sweeps and down-409 sweeps present equivalent (and thus directly comparable) production challenges; and 410 (iv) the performance required for frequency modulations varies linearly across the 411 frequency scale. These assumptions are likely oversimplified, and we welcome user-412 guided adjustments and re-weightings in how FEX is calculated. As an illustration, 413 consider the fourth assumption above. Our decision to use a linear scale to code 414 frequency for our FEX calculations was motivated mainly by an interest in retaining a 415 common scale with spectrograms, which employ linear frequency scales and on which 416 visual descriptions of FEX calculations can be overlaid (Fig. 2). However, as was 417 recently argued by Cardoso (2013b), performance indices involving frequency

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418 comparisons (including both FEX and VDEV) might also be conducted using frequency 419 data that is first log-transformed, in part because use of linear frequency scales might 420 overestimate vocal performance at higher frequencies. If, to illustrate, doubling a source 421 frequency requires similar performance across the frequency scale, then a bird 422 modulating its song from 2 kHz to 4 kHz would gain four times the performance "credit" 423 as compared to a transition from 0.5 kHz to 1 kHz. Ideally, decisions about whether to 424 log-transform frequency data before calculating performance values will be guided not 425 just by theory but also by empirical studies that explore relationships between vocal 426 mechanics and song frequency variation (e.g., Goller & Suthers 1996; Hoese et al. 427 2000; Nelson et al. 2005; Riede et al. 2006). In any case, to facilitate further exploration 428 of the outcomes of linear versus log-transformed frequency scaling, we offer users a 429 log-transformation option in FEX calculator.

430 Returning the present analyses: The first main question we asked was how the 431 frequency excursion and vocal deviation indices compare as measures of vocal 432 performance. The generally strong relationships between the two performance indices 433 indicates that they overlap in aspects of vocal performance that they capture. However, 434 inspection of the phonological structure of songs, with reference to regression plots (Fig. 435 3), illustrates how frequency excursion indeed captures additional, finer-scale aspects of 436 vocal performance. In particular, songs that map above the regression lines tend to 437 have relatively rapid frequency modulations and large frequency jumps between notes, 438 features that are overlooked by vocal deviation (e.g., Fig. 1A and C). By contrast, 439 songs with slower, more gradual frequency modulations and less abrupt frequency 440 transitions between notes map comparatively low in frequency excursion (Fig. 1B & D).

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441 Both of our indices revealed species differences in vocal performance. Following vocal 442 deviation, chipping sparrows sang with the highest performance, swamp sparrows with 443 intermediate performance, and song sparrows with the lowest performance. Frequency 444 excursion also places song sparrows as the poorer performers, but lumps chipping 445 sparrows and swamp sparrows as equivalent performers. These results correspond 446 roughly to body size, with the largest-bodied species achieving the lowest performance. 447 This contrasts the results of a larger analysis of multiple sparrow species, which failed 448 to identify a body-size effect on vocal deviation (Podos 2001). Species difference in 449 vocal performance might also arise from varying strengths of sexual selection on vocal 450 performance. Consistent with this possibility are data showing that both chipping and 451 swamp sparrows attend to inter-male variation in vocal performance (as measured by 452 trill rate or vocal deviation, Moseley et al. 2013; Goodwin & Podos 2014), whereas in 453 song sparrows, song assessment seems based mainly on non-performance features 454 such as song type matching and soft song (Searcy et al 2014). With this latter point, we 455 acknowledge that further work would be needed with song sparrows to test directly the 456 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

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464 juncos: the frequency excursion index varied significantly by song type but not by bird, 465 with the effect size of song type being notably larger. Notably, these distinctions were 466 not detected by the vocal deviation metric. To the extent that song types are less 467 variable than individuals in vocal performance, the value of individual songs as 468 indicators of signaler attributes related to vocal capacity should be compromised 469 (Cardoso et al. 2009). However, our analysis did not take into account song type use, 470 i.e., whether birds tend to use songs with different performance levels in different 471 singing contexts.

472 We also detected relationships between song sharing and vocal performance, in the 473 direction opposite to that expected (and again with stronger effects for frequency 474 excursion). Overall, songs that were shared tended to be lower performance, and our 475 initial assumption that song sharing would promote the evolution of higher performance 476 (Logue & Forstmeier 2008; see also Poesel & Nelson 2015) is thus unsupported. 477 Perhaps the unshared, higher performance songs are used rarely, and reserved for the 478 most critical social interactions. Moreover, if young birds are unable to produce high-479 performance song types with accuracy, then perhaps they preferentially crystallize 480 lower-performance songs, which would increase the prevalence of low-performance 481 songs in a population and, correspondingly, the likelihood that they would be shared. Of 482 particular interest in future work will be attention to the interplay of song performance 483 and song use in species like swamp sparrows that have song repertoires (as in DuBois 484 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

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487 excursion values were greater for trilled as compared to non-trilled song segments, in 488 the predicted direction, this difference was not statistically significant. It thus seems that 489 song sparrows do not achieve higher performance in trills, at least as measured by 490 frequency excursion. One possible explanation for this outcome is that selection on trill 491 performance in song sparrows might be comparatively weak, at least as compared to 492 our other two study species for which available data suggests that trills are both 493 mechanically limited and scrutinized in field contexts. Further studies comparing the 494 performance of trilled versus non-trilled songs or song segments should include 495 additional species, particularly those with evidence for relying on performance variation 496 in vocal communication. Nightingales (Luscinia megarhychos) would seem like a 497 particularly good candidate species, given that they seem to sing with high performance 498 and also produce both trilled and non-trilled song segments (Kunc et al. 2006) 499 Overall, we envision frequency excursion being applied to these and other questions 500 about vocal performance, including questions previously addressed using other

501 performance measures such as trill rate and vocal deviation. Some such questions

502 concern the relationship between ecology, morphology, and vocal signal structure (e.g.,

503 Slabbekoorn & Smith 2000; Podos 2001; Seddon 2005; Derryberry et al. 2012;

504 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;

507 Podos 1997; Cardoso & Hu 2011; Wilson et al. 2014).

508

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- Bradbury, J. W. and Vehrencamp, S. L. 2011. *Principles of Animal Communication*. Sinauer
 Associates.
- Brumm, H. and Slater, P. J. B. 2006. Ambient noise, motor fatigue, and serial redundancy in
 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
- 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 Ageliaus 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.
- 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.
- **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.

Hartley, R. S. and Suthers, R. A. 1989. Airflow and pressure during canary song: evidence for
 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
- of Darwin's finches (Geospiza fortis). *Biological Journal of the Linnean Society*, 88, 489498.
- 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.
- Janicke, T., Hahn, S., Ritz, M. S. and Peter, H. U. 2008. Vocal performance reflects individual
 guality 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.
- Lahti, D. C., Moseley, D. L. and Podos, J. 2011. A tradeoff between performance and
 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.
- 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

ornaments. *American Naturalist*, 172, 34-41.

- Marler, P. and Peters, S. 1982. Structural changes in song ontogeny in the Swamp Sparrow
 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.
- Nowicki, S., Peters, S. and Podos, J. 1998. Song learning, early nutrition and sexual selection
 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.
- Podos, J., Peters, S. and Nowicki, S. 2004a. Calibration of song learning targets during vocal
 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.
- Poesel, A. and D.A., N. 2015. Changes in performance of shared and unshared songs within
 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
- during close-range vocal competition in gray tree frogs *Hyla versicolor. American Naturalist,*180, 425-437.
- 659 **Riede, T. and Goller, F.** 2014. Morphological basis for the evolution of acoustic diversity in
- 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
- 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.
- Sakata, J. T. and Vehrencamp, S. L. 2012. Integrating perspectives on vocal performance and
 consistency. *Journal of Experimental Biology*, 215, 201-209.
- 666 Schmidt, R., Kunc, H. P., Amrhein, V. and Naguib, M. 2008. Aggressive responses to
- broadband trills are related to subsequent pairing success in nightingales. *Behavioral 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
- Hammerschmidt, K. 2010. The central importance of information in studies of animal
 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*

687 *Ecology*, 22, 1-9.

688 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.
- 700 Vehrencamp, S. L., Bradbury, J. W. and Gibson, R. M. 1989. The energetic cost of display in
- 701 male sage grouse. *Animal Behaviour,* 38, 885-896.
- 702 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.

- 704 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*

706 *Experimental Biology*, 182, 147-171.

707 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-

709 186.

- Wilson, D. R., Bitton, P. P., Podos, J. and Mennill, D. J. 2014. Uneven Sampling and the
 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
- 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:
- implications for birdsong production. *Proceedings of the Royal Society of London*
- 720 Series B-Biological Sciences, 271, 483-491.

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721 Table 1. Song type x bird performance scores for our swamp sparrow sample (A=vocal deviation; B=frequency excursion). Descriptive statistics (mean,

522 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,

Vocal deviation x song type, 19.19, Frequency excursion x bird, 27.21, Frequency excursion x song type, 16.69.

724

A. Vocal deviation:

726

Bird ID

Song Type	1	2	3	4	5	6	7	8	9	10	11	12	means:	stdev:	CV:
А	1.92												1.92		
В			2.52					2.02	2.86				2.47	0.42	17.1
С						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
н					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
К	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						

Table 1 continued:

729

730 B. Frequency excursion:

731

Bird ID

Song ype	1	2	3	4	5	6	7	8	9	10	11	12	means:	stdev:	CV:
А	211.2												211.24		
В			102.6					96.1	101				99.89	3.36	3.37
С						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
Е		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
Н					150.7		127.8					142.2	140.22	11.55	8.23
Ι		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
К	139.5		176.8		121.3								145.87	28.29	19.39
L		297.7											297.71		
	156.4	201.6	144.0	122.0	1 1 1 1	1 - 0 - 7	125.6	112.0	125.0	170.6	170 1	142.2	-		
neans:	150.4	201.6	144.0	133.8	141.4	158.7	125.0	112.9	135.8	170.6	179.1	142.2			
staev:	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
- 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

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740 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.

748

749 Figure 2. Plots illustrating how frequency excursion is calculated, for a single song clip, in FEX calculator. 750 (A) Grevscale spectrogram of song segment from a male Adelaide's warbler, recording courtesy of 751 David Logue. The clip is 0.65 s in duration, and the y-axis shown (zoomed in here for illustration 752 purposes) ranges from 2.05 to 8.03 kHz. (B) All points from this clip with energy above our dB threshold, 753 and thus eligible to be included in the frequency excursion calculation. Note that most but not all 754 background noise is excluded in this step; (C) The highest amplitude points per time bin, after manual 755 de-selection of candidate highest-amplitude points that the user identified as having captured noise or 756 inter-note intervals rather than actual vocal output; (D) Highest-amplitude points now connected by line 757 segments. The cumulative length of the line segments divided by total time interval is the frequency 758 excursion value. For this song segment, the cumulative path length is 45.17, segment duration (first to 759 last highest-amplitude points) is 0.607 s, and the resulting frequency excursion value is 74.42.

760

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.

766

767 Figure 4. Average vocal performance of swamp sparrow song types plotted against the number of birds in 768 our sample who shared those types. Left panels show data when song sharing is calculated within the 769 sample only, and right panels show data when song sharing is calculated across the population at large. 770 In all cases, song performance declines as the incidence of song sharing increases. The relationship 771 approaches statistical significance for the upper left panel data, and achieves statistical significance for 772 the other three panels (see text). The direction of the observed relationship contradicts our expectation 773 that shared song types would tend to require higher performance. 774 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.
- 777
- 778
- 779

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781 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 configuring, FEX building. installing, and using 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

- 833 it can be followed by up to 4 floating point numbers specifying the coefficients for a generalized 834 cosine windowing function. 835 836
 - 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 user 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

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3.1 Overview

855 The FEX calculator package contains two executable files: the compiled binary fex and a python script 856 front-end fex-gtk. In most cases, only fex-gtk should be used directly. Details of FEX calculator are 857 provided in the manual page distributed with the software.

858 Fex-gtk is a front-end of the program that facilitates batch processing of large numbers of wave files. 859 Fex-gtk can be provided a list of file names, or can be run with no parameters to trigger a dialog window 860 to select wave files. FEX calculator will be run on each input file, and the results can either be stored to a 861 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

875 The steps below outline a recommended approach to analysing a song in FEX calculator. The key 876 binding or controls for each step are listed as bullet points under that step. Many controls specify a 877 direction which can be indicated with the keyboard arrow keys, home-row directional keys (h, j, k, l), 878 or with a 2-axis mouse scroll-wheel. Many controls also specify a modifier key to be held down with the 879 key or directional indicator. Press 'F1' at any time in Fex to open a help window outlining these and other 880 controls. 881

- 1. Crop out the region of interest. Everything outside of the selected region will 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

- 890
 2. Optionally adjust the floor value as desired. This will only affect the display of the background
 891 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.

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<u> </u>

- 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 {
58	doub∎e **amp;
	double *time;
70	double *freq;
	double max, min;
72	int nfreq, ntime;
	char **mask;
74	} 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) {
26
      /* a//ocate memory */
     FFT *fft = (FFT *) calloc(1,sizeof(FFT));
28
     fft->nfreq = conf.winlen/2 + 1;
     fft->ntime = wav->samples/conf.hop;
30
     fft->amp = (double **) calloc(fft->ntime, sizeof(double *));
     fft->time = (double *) calloc(fft->ntime, sizeof(double));
32
     fft->freq = (double *) calloc(fft->nfreq, sizeof(double));
34
     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 */
36	<pre>double nyquist = (double) wav->rate / 2000.0;</pre>
	<pre>double df = nyquist / fft->nfreq;</pre>
38	<pre>double dt = (double)wav->samples / (double)(wav->rate * fft->ntime);</pre>

```
double f, t;
40 int i, j;
for (i = 0, f = 0.0; i < fft->nfreq; i++, f += df) fft->freq[i] = f;
42 for (i = 0, t = 0.0; i < fft->ntime; i++, t += dt) fft->time[i] = t;
```

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.

```
/* prepare fftw */
     fftw_complex *in, * out;
44
     fftw_plan p;
     in = (fftw_complex *)fftw_malloc(conf.winlen * sizeof(fftw_complex));
46
     out = (fftw_complex *)fftw_malloc(conf.winlen * sizeof(fftw_complex));
     p = fftw_plan_dft_1d(conf.winlen, in, out, FFTW_FLAGS);
48
        create windowing function */
     double window[conf.winlen];
50
     double *a = conf.win->a;
52
     double wl = conf.winlen;
     for (i = 0; i < conf.winlen; i++)</pre>
        window[i] = a[0] - a[1] * cos(2 * M_PI * (i / (wI - 1.0))) +
54
               a[2] * cos(2 * M_PI * (i / (wI - 1.0))) ·
               a[3] * cos(2 * M_PI * (i / (wl - 1.0)));
56
```

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).

```
/* /oop over signa/ */
     int pos;
58
     for (pos = 0, j = 0; pos < wav->samples; pos += conf.hop, j++) {
         fft->amp[j] = (double *) malloc(fft->nfreq * sizeof(double));
60
         fft->mask[j] = (char *) calloc(fft->nfreq, sizeof(char));
          * copy windowed chunk to dat */
62
         for (i = 0; i < conf.winlen; i++) {</pre>
            if (pos + i < wav->samples) {
64
               in[i][0] = wav->d[pos + i] * window[i];
               in[i][1] = 0.0;
66
            }
68
            else {
               in[i][0] = 0.0;
               in[i][1] = 0.0;
70
               goto doublebreak;
            }
72
         }
         /* calculate fft & fill amp matrix */
74
         fftw_execute(p);
        for (i = 0; i < fft->nfreq; i++)
76
            fft->amp[j][i] = sqrt(out[i][0] * out[i][0] +
                  out[i][1] * out[i][1]);
78
      }
```

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.

1074

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

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.

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

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.

```
typedef struct Spectro {
    const char *fname;
    char *name;
    unsigned char *a_spec, *a_thresh;
    cairo_surface_t *m_spec, *m_thresh, *s_points;
    FFT *fft;
    int fft_x, fft_y, fft_w, fft_h, fft_lo, fft_hi;
    double pex, tex, fex;
    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 It and If (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 and zeroed. pex tex are

1	1	36
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1	1	58
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1	1	60
T	1	00
1	1	61
1	1	62

```
126 int spectro_points() {
      if (spect->s_points) cairo_surface_destroy(spect->s_points);
      spect->s_points = cairo_image_surface_create(CAIRO_FORMAT_ARGB32,
128
            spect->fft_w * conf.scale, spect->fft_h * conf.scale);
      cairo_t *p = cairo_create(spect->s_points);
130
      cairo_t *I = cairo_create(spect->s_points);
132
      set_color(p,RGBA_POINTS);
      set_color(l,RGBA_LINES);
      int i, j, f;
134
      double lt = spect->fft->time[0], lf = spect->fft->freq[0];
      spect - pex = 0.0;
136
      spect \rightarrow 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 **It**, **If** to the current point's time-frequency coordinate. **It** and **If** 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.

```
/* loop through time bins */
138
      for (i = spect->fft_x; i < spect->fft_w + spect->fft_x; i++) {
           i* Find maximum (non masked) Frequency in time bin */
          for (f = 0, j = spect->fft_y; j < spect->fft_h+spect->fft_y; j++) {
                if (spect->fft->mask[i][j]) continue;
                 if (spect->fft->amp[i][j] > spect->fft->amp[i][f] || !f)
                  f = j;
         }
         /* add points and do calculations if f is above threshold */
           if (f > 0 && spect->fft->amp[i][f] > conf.thresh) {
            if (It != spect->fft->time[0]) {
                spect->pex += sqrt(
                   (spect->fft->freq[f] - If) * (spect->fft->freq[f] - If) +
(spect->fft->time[i] - It) * (spect->fft->time[i] - It) );
               spect->tex += spect->fft->time[i] - It;
            3
            It = spect->fft->time[i];
            If = spect->fft->freq[f];
            cairo_line_to(l,
                    (i - spect->fft_x) * conf.scale + conf.scale / 2,
                   (f - spect->fft_y) * conf.scale + conf.scale / 2);
            cairo_new_sub_path(p);
            cairo_arc(p,
                    (i - spect->fft_x) * conf.scale + conf.scale / 2,
                   (f - spect->fft_y) * conf.scale + conf.scale / 2,
                    conf.col[RGBA_POINTS].w,0,2*M_PI);
         }
         spect->fex = spect->pex / spect->tex;
     }
      cairo_fill(p);
      cairo_stroke(1);
      cairo_destroy(p);
      cairo_destroy(I);
      return 0;
172 }
```

1198

1199



Frequency

Time



time







category