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Breeding bird density does not drive vocal individuality

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Abstract Many species produce individually specific vocalizations and sociality is a hypothesized driver of such individuality. Previous studies of how social variation influenced individuality focused on colonial or non-colonial avian species, and how social group size influenced individuality in sciurid rodents. Since sociality is an important driver of individuality, we expected that bird species that defend nesting territories in higher density neighborhoods should have more individually-distinctive calls than those that defend nesting territories in lower-density neighborhoods. We used Beecher's information statistic to quantify individuality, and we examined the relationship between bird density (calculated with point-counts) and vocal individuality on seven species of passerines. We found non-significant relationships between breeding bird density and vocal individuality whether regressions were fitted on species values, or on phylogenetically-independent contrast values. From these results, we infer that while individuality may be explained by social factors, breeding bird density is unlikely to be generally important in driving the evolution of individually-specific vocalizations [*Current Zoology* 58 (5): 761–768, 2012].

Keywords Individuality, Sociality, Birdsong, Breeding bird density

The ability to discriminate individuals based on their vocalizations can be important to receivers (e.g., Stoddard et al., 1991; Rendall et al., 1996; Weiss et al., 2001; Blumstein and Munos, 2005) and to signalers (Sayigh et al., 1990; Rendall et al., 1996; Weiss et al., 2001). For vocal species, the ability to discriminate among individuals depends on the amount of variation within and among individuals. If individuals within a species exhibit large amounts of variation within their own calls, relative to the variation among individuals, then these individuals cannot be discriminated (Puglisi and Adamo, 2004). By contrast, a relatively low amount of intra-individual variation relative to inter-individual variation is necessary for individual identification (Terry and McGregor, 2002).

The degree of individuality present within a vocalization can be quantified using Beecher's information statistic (Beecher, 1989; Blumstein and Munos, 2005; Pollard et al., 2010; Pollard and Blumstein, 2011). This statistic, derived from information theory, quantifies individuality by calculating a numerical value in bits (Beecher, 1989). The higher this value is for a given vocalization, the more individuality present in the vocalization. Thus, higher Beecher information statistic values indicate higher levels of inter-individual variation relative to intra-individual variation. Beecher's information statistic can be used to analyze vocalizations and determine which vocalizations are best suited for positively identifying individuals within a species (Pollard et al., 2010).

Beecher's information statistic has also been used to examine the relationship between sociality and individuality, assuming that more social species derive greater benefits from producing individually distinctive vocalizations (Beecher, 1982; Beecher, 1989; Medvin et al., 1993). Indeed, Beecher (1988) discovered that non-colonial swallow species, exhibit a lower degree of individuality in their parent-offspring recognition vocalizations, in comparison to colonial swallows. In another study, Pollard and Blumstein (2011) found that more social ground-dwelling sciurid rodents have more individually-distinctive calls.

Many species defend territories during the breeding season. Some of these species are social during the non-breeding season, while others are not particularly social (Ammon, 1995; Chilton et al., 1995). If sociality can select for individual recognition, it is reasonable to assume that species that typically live in denser neighborhoods might be selected to produce more individually-distinctive calls and songs than those living in

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less dense neighborhoods. This may prove advantageous for birds discriminating neighbors from strangers (Baker et al., 1981; Stoddard et al., 1991), subspecies (Petrinovich and Patterson, 1981), and dialects (Thompson and Baker, 1993), as well as aiding females in how they evaluate song (Baker et al., 1987; Bateson and Healy, 2005). However, a potential constraint on this putative relationship might emerge in songbirds who learn their songs prior to dispersal and for whom neighborhood density varies between years.

The aim of our study was to examine the relationship between breeding bird density and vocal individuality. We focused on seven abundant species of passerines that lived sympatrically in a sub-alpine valley in Colorado. To identify the relationship between vocal individuality and density, we recorded birds and calculated Beecher's information statistic. We performed point counts to examine the relative density of each species locally. We expected that the species living in higher density populations would have a greater Beecher information statistic.

1 Materials and Methods

1.1 Recording and measuring songs

Species considered in this study included free-living green-tailed towhees *Pipilo chlorurus*, Lazuli buntings *Passerina amoena*, Lincoln's sparrows *Melospiza lincolnii*, mountain white-crowned sparrows *Zonotrichia leucophrys oriantha*, American robins *Turdus migratorius*, house wrens *Troglodytes aedon*, and warbling vireos *Vireo gilvus* in and around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, U.S.A (38° 57′46″N 106° 59′34″W). Observers walked around the town site and the surrounding area listening for males singing. Each individual was then approached and common songs were recorded using a Sennheiser MZW 816 or ME-67 microphone (Sennheiser Electronic, Wedemark, Germany) onto a Marantz Professional Solid State Recorder PMD660 (D&M Professional, Itasca, Illinois, U.S.A.). The distance between the bird and the microphone varied from 5m to 30 m due to the varying tolerance of each individual to our approach. We aimed to record common songs from ten males of each species, with at least 20 good-quality songs from each subject male. However, some songs were of insufficient quality for subsequent analysis so final sample sizes are reduced for some species (Table 1). Given that these species were highly territorial, we are confident that recordings made in different locations were from different birds. We worked a 6 km section of the upper East River valley and walked up to 400 m away from the road that bisects it. In addition, two different birds could be recorded in the same area during the same day only when the observers could be certain that they were separate individuals. No recordings took place during rain or wind to ensure the highest signal to noise ratio.

Table 1 Recording dates per species and number of individuals recorded per day (in parentheses)

Species	Recording Dates
House Wren	21 Jun 2011(1), 24 Jun 2011(2), 25 Jun 2011(2), 27 Jun 2011(1), 29 Jun 2011(1), 30 Jun 2011(3)
Lazuli Bunting	23 Jun 2011(2), 26 Jun 2011(2), 27 Jun 2011(2), 29 Jun 2011(2), 2 Jul 2011(1), 3 Jul 2011(1)
American Robin	30 May 2009(1), 01 Jun 2009(1), 04 Jun 2009(1), 05 Jun 2009(1),07 Jun 2009(1), 08 Jun 2009(1), 09 Jun 2009(2), 14 Jun 2009(1), 15 Jun 2009(1),
Warbling Vireo	27 Jun 2011(2), 29 Jun 2011(2), 30 Jun 2011(2), 3 Jul 2011(1), 5 Jul 2011(1), 10 Jul 2011(1), 25 Jul 2011(1)
Green-tailed Towhee	20 Jun 2011(2), 23 Jun 2011(1), 27 Jun 2011(1), 29 Jun 2011(1), 30 Jun 2011(1), 01 Jul 2011(1), 05 Jul 2011(1), 07 Jul 2011(1), 15 Jul 2011(1), 23 Jul 2011(1)
Lincoln's Sparrow	11 Jun 2010(1), 14 Jun 2010(1), 15 Jun 2010(1), 16 Jun 2010(1), 18 Jun 2010(1), 21 Jun 2010(1), 23 Jun 2010(1), 24 Jun 2010(1), 30 Jun 2010(1), 01 Jul 2010(1)
White-crowned Sparrow	18 Jun 2010(1), 20 Jun 2010(1), 22 Jun 2010(1), 24 Jun 2010(1), 25 Jun 2010(1), 28 Jun 2010(1), 29 Jun 2010(1), 06 Jul 2010(1), 07 Jul 2010(1), 09 Jul 2010(1).

Sound files were analyzed using Praat sound analysis software (Phonetic Sciences, University of Amsterdam, Amsterdam, Netherlands). Recordings were normalized to 95% peak amplitude. Preliminary examination of spectrograms (Fourier transformed spectrograms, Praat parameter details: 0–10 kHz frequency range, spectrogram window length = 0.005 s, dynamic range = 40 dB, time steps = 1000, frequency steps = 250) helped us identify possible attributes to measure. Each species had unique songs; hence we measured a different set of variables for each one of them to capture sufficient variation. Measurements are summarized in the Supplementary material. While this problem of not entirely comparable data sets is unavoidable given the diversity of songs, the analysis described below only focuses on those variables/factors that are individually variable.

We used a principal component analysis in SPSS 20 (IBM Inc., 2011; MINEIGEN = 0.01, ITERATE = 25, NOROTATE, METHOD = CORRELATION) to reduce the data to uncorrelated factors. We then fitted an ANOVA model where we blocked by individual to each factor and retained *F*-values that were significant ($P <$ 0.05). These *F*-values were used to calculate the Beecher information statistic for each species (Beecher, 1989; Blumstein and Munos, 2005; Pollard et al., 2010).

While there is no *a priori* reason to expect that more traits measured should inevitably lead to greater information statistic values, we evaluated this hypothesis by correlating the Beecher information statistic with the number of traits measured, the number of factors extracted, and the number of significant factors extracted. We found no large or significant relationships between the number of traits and the information statistic (r = -0.401, P = 0.373), the number of factors and the information statistic (r = -0.614, P = 0.143), nor the number of significant factors and the information statistic (r = 0.149, P = 0.749). However, species with more traits, had more factors extracted (r = 0.869, P = 0.001), but there was no relationship between the number of traits measured and the number of significant factors (r = -0.322, P = 0.482). Thus, we feel confident that our measures reflect variation among species and are not an artifact of the different numbers of measurements made for each species.

Because birds were not individually identified, we were unable to re-record individuals and thus our estimates of individuality must be viewed as an index. However, because our methods were consistently applied to all species, there should be no bias for different species. Thus, even if we underestimated the true variation in a given species, all species values were estimated similarly, and thus our consistent method should generate a similar rank order for subsequent analysis.

1.2 Estimating species density

To estimate breeding bird density, we used point counts, taken at twelve different locations in July 2011. These points extended 4 km south of the RMBL, along both sides of the road, and were separated by at least 200 m from one another. Six of these were in open grass-willow meadows, and six were in aspen patches, in order to cover the diversity of habitat types that the species inhabited. Point counts were repeated six times at each site. Before each point count started the observers waited three minutes during which they were silent and immobile. During the following 10 min we recorded the species and radial distance of every bird seen or heard. Point count data were analyzed in DISTANCE 6.0 release 2 (Thomas et al., 2010). We contrasted three models to determine the best estimate: hazard rate, half-normal key and uniform key (Buckland et al., 1993). The best-fitting model (lowest AIC value) for each species was then used in our density data (Table 2).

Table 2 Breeding bird density & Beecher Information Statistics by species

Species	Habitat	Density (N/ha)	Density CV	Encounter Rate (N/min)	Model	Beecher Information Statistic
White-crowned Sparrow	OA	0.46	0.36	0.06	Hazard-rate Key	8.8
Lincoln's Sparrow	OA	0.26	0.17	0.08	Uniform Key	6.8
Green-tailed Towhee	OA	0.14	0.22	0.05	Uniform Key	5.1
Lazuli Bunting	OA	0.19	0.17	0.06	Uniform Key	10.6
House Wren	AP	0.78	0.15	0.14	Half-normal Key	10.1
Warbling Vireo	AP	0.08	0.005	0.06	Uniform Key	2.3
American Robin	All	0.91	0.44	0.10	Hazard-rate Key	3.2

Habitat is scored as open grass-willow meadows (OA) and aspen patches (AP)

1.3 Quantifying the relationship between density and individuality

We regressed breeding bird density against individuality both on raw data, and on phylogenetically independent contrast values (Felsenstein, 2004). Our phylogeny, derived from a family-level phylogeny (Carson and Spicer, 2003; Spancer and Dunipace, 2003) was: ((((Lazuli bunting, (('green-tailed towhee', 'Lincoln''s sparrow'), 'white-crowned sparrow')), house wren), American robin), warbling vireo).

2 Results

Beecher information statistic values ranged from lower values, for Warbling Vireos (2.3) and American Robins (3.2), to higher values for House Wrens (10.1) and Lazuli Buntings (10.6) (Table 2). Breeding bird estimates varied from 0.08birds/ha (Warbling Vireos), to 0.91/ha (American Robins) (Table 2). However, regardless of how the data were examined, for these species at this location, there was no relationship between breeding bird density and vocal individuality (raw data R = 0.101, *P* = 0.829; phylogenetically independent contrasts R = 0.128, *P* = 0.784).

3 Discussion

Taken together, we found no support for the hypothesis that vocal individuality, measured using Beecher's information statistic, covaries with the density of breeding conspecifics. Thus, while previous work has shown strong associations between sociality and vocal individuality in colonial versus non-colonial birds (Medvin and Beecher, 1986; Beecher, 1988), and in sciurid rodents (Pollard and Blumstein, 2011), our study suggests that the relationship between sociality and individuality may not extend to breeding bird densities.

Pollard and Blumstein (2012) introduced a trait-based view of the evolution of complex vocal communication. They noted that demographic complexity drives alarm call repertoire size evolution, and group size drives the evolution of vocal individuality, but not vice-versa. This trait-based view of vocal evolution is valuable because it allows us to identify key drivers of the multiple attributes of any given signal.

Thus, while the density of conspecifics may influence other aspects of vocal structure (e.g., amplitude Brumm and Zollinger, 2011), our results suggest that it does not strongly influence the evolution of vocal individuality, at least for the species and methods employed. It is possible that with a larger sample size, the apparently weak relationship may become significant. Remarkably, however, the effect of group size on the individuality of sciurid rodent alarm calls is quite large (Pollard and Blumstein, 2011) and we expected, given those results, to detect an effect, if present, with a study of seven species. However, weak effects are known with respect to other vocal traits. For instance, the acoustic adaptation hypothesis (Morton, 1975) predicts that a species' vocalization will be best transmitted in its own environment. While this is a very reasonable expectation, results from a formal meta-analysis have shown that this effect is small (Boncoraglio and Saino, 2007).

It is likely that the nature of the information being transmitted (alarm, territorial advertisement, mate attraction, etc.) may influence the value of individually-specific information. From this perspective, the magnitude of the effect size of the relationship between group size and individually-specific alarm calls (Pollard and Blumstein, 2012) compared to the effect size of density and territorial song in the present study, may highlight the importance of receivers extracting immediate information about the true probability of predation which may vary according to caller reliability (Hare and Atkins, 2001; Blumstein et al., 2004). By contrast, hearing a territorial intruder does not create the same urgency to respond immediately. Despite this, we do see quite a bit of variation in individuality among these birds; a phenomenon that begs further investigation.

Our results suggest that there is no effect of breeding bird density on individuality in territorial call among the bird species examined or, if existent, it is quite small. Yet, we know that bird species vary extensively in terms of vocal individuality. Thus, future studies, perhaps with more species and certainly with other traits, are required to identify evolutionary drivers of vocal individuality in breeding birds.

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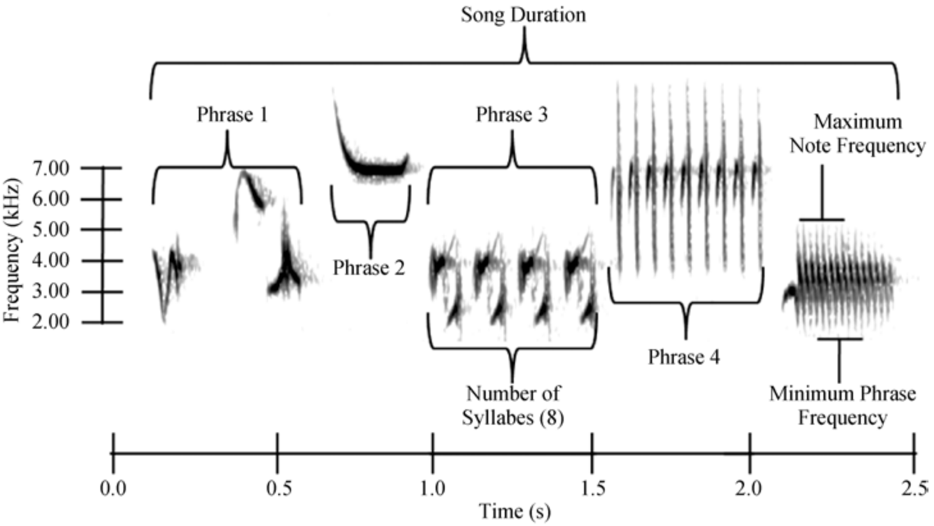
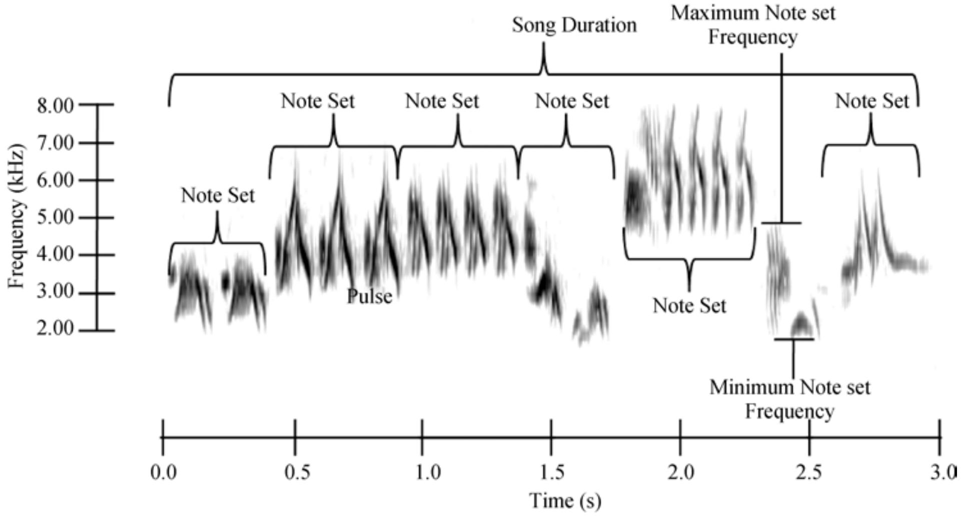
Supplementary Material: Details of Measurements Made on Songs

STable 1 Acoustic measurements made for each species

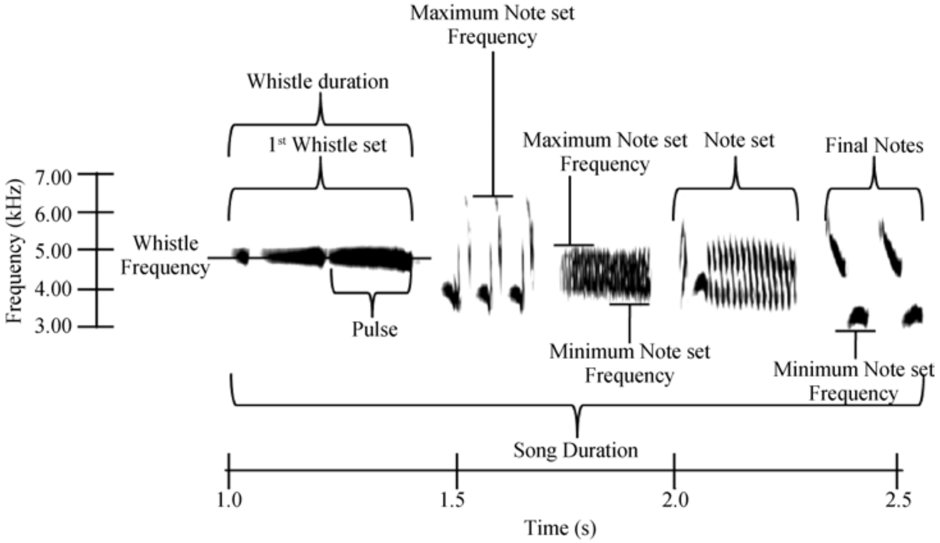
Green-tailed Towhee (Fig. 1)	**Number of variables:** 55. **Song Measures:** 1) Duration, 2) No. Phrases, 3) Total syllables, 4) Song rate (No. Syllables/song duration), 5) Max. freq, 6) Min. freq, 7) Bandwidth; **Phrase Measures (Phrases 1-6):** 1) Duration, 2) No. of syllables, 3) Max. freq, 4) Min. freq, 5) Mean 1st formant, 6) 1st Formant at max Amplitude, 7) Phrase rate (No. Syllables/phrase duration), 8) Bandwidth.
Lincolns' Sparrow (Fig. 2)	**Number of variables** 44. **Song Measures:** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Number of note sets. **Note set Measures (Note set 1-10):** 1) Duration, 2) Number of notes, 3) Max. freq, 4) Min. freq.
White-crowned Sparrow (Fig. 3)	**Number of variables:** 33. **Song Measures:** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Number of note sets. **Whistle Measures:** 1) Frequency, 2) No. of whistle pulses (1st set), 3) No. of whistle pulses (2nd set), 4) duration, 5) Pulse Duration. **Note set Measures (Note set 1-3):** 1) Duration, 2) Max. freq, 3) Min. freq, 4) No. of terminal notes.
Lazuli Bunting (Fig. 4)	**Number of variables:** 26. **Song Measures:** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Bandwidth, 5) Number of syllables, 6) Number of trills. **Phrase Measures (Phrase 1-4):** 1) Duration, 2) Number of syllables, 3) Max. freq, 4) Min. freq. 5) Bandwidth, 6) 1st Formant at max Amplitude.
House Wren (Fig. 5)	**Number of variables:** 25. **Song Measures:** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Bandwidth, 5) Number of syllables, 6) No. of motifs, 7) No. of high low transitions. **Phrase Measures (Note set 1-2):** 1) Duration, 2) Number of syllables, 3) Max. freq, 4) Min. freq, 5) Bandwidth, 6) 1st Formant at max Amplitude. **Bubbly phrase Measures:** 1) Duration, 2) Number of syllables, 3) Max. freq, 4) Min. freq, 5) Bandwidth, 6) 1st Formant at max Amplitude.
Warbling Vireo (Fig. 6)	**Number of variables:** 87. **Song Measures:** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Number of syllables, 5) Bandwidth, 6)Song rate (No. Syllables/song duration). **Syllable Measures (Syllable 1-9):** 1) Duration, 2) Number of notes, 3) Max. freq, 4) Min. freq, 5) Bandwidth, 6) Mean 1st formant, 7) 1st Formant at max Amplitude, 8) Phrase rate (No. Syllables/phrase duration), 9) Bandwidth.
American Robin (Fig. 7)	**Number of variables:** 24. **Song Measures:** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Number of syllables. **Syllable Measures (Syllable 1-4):** 1) Duration, 2) Max. freq, 3) Min. freq, 4) Bandwidth, 5) 1st formant at max. freq.



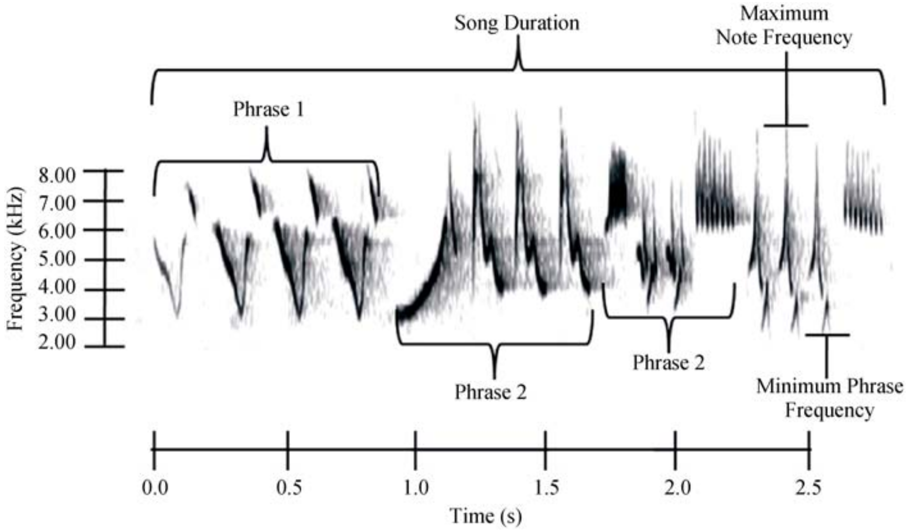
SFig. 1 Measures made on Green-tailed Towhee song



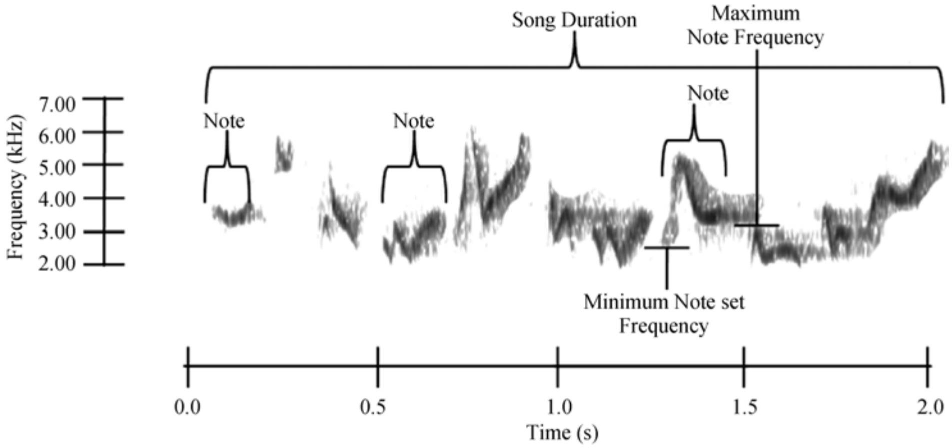
SFig. 2 Measures made on Lincoln's sparrow song



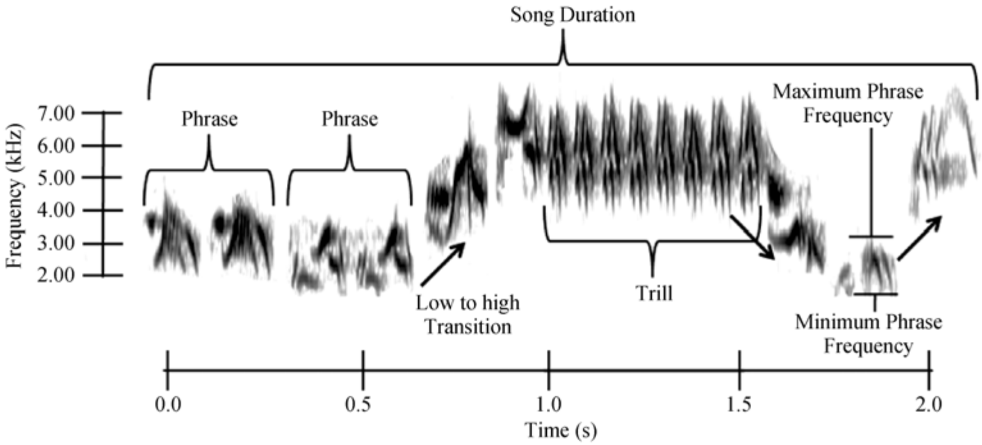
SFig. 3 Measures made on white-crowned sparrow song



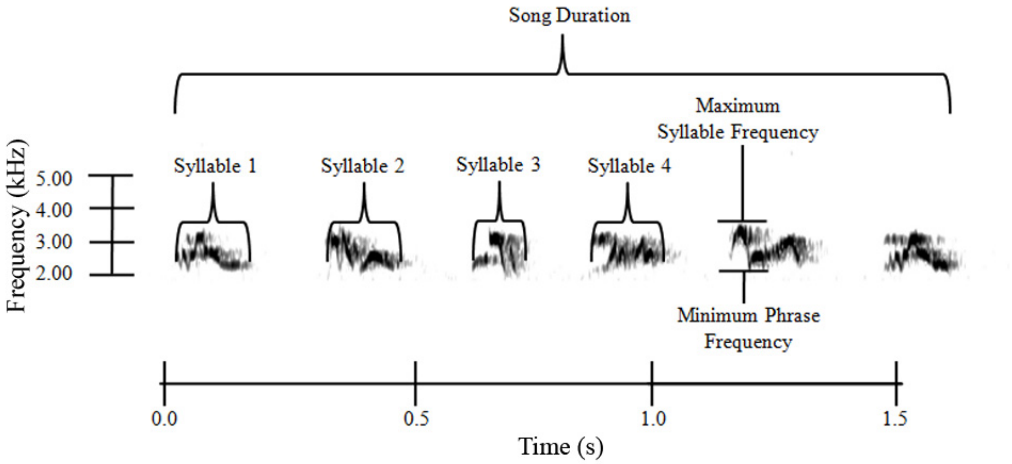
SFig. 4 Measures made on Lazuli bunting song



SFig. 5 Measures made on house wren song.



SFig. 6 Measures made on warbling vireo song



SFig. 7 Measures made on American Robin song