

Does breeding bird density drive vocal individuality?

Douglas R. McClain

Mentor: Dr. Daniel T. Blumstein

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Abstract

Many species produce individually specific vocalizations and sociality is a hypothesized driver of individuality. Previous studies of social variation focused on species that were colonial nesters or not, and social group size in sciurid rodents. If sociality is an important driver of individuality, we might expect that 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 nesting density and vocal individuality in Lincoln's sparrows, *Melospiza lincolnii*, and mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*. We conducted point counts to examine the relative density of each species at our site and conducted a literature review to examine relative densities of each species at other sites. We found that mountain white-crowned sparrows exhibited a significantly greater degree of individuality within their songs than did Lincoln's sparrows. While there was no difference in density of the two sparrow species at our study site, the literature review suggested that the relative density of white-crowned sparrows is typically greater than Lincoln's sparrows. From this we conclude that white-crowned sparrows are generally more social than Lincoln's sparrows, and that, as predicted, they have a greater degree of individuality in their vocalizations. Thus, we suggest that bird species nesting in denser aggregation exhibited a greater degree of vocal individuality. With further work, it may be possible to use Beecher's information statistic as a potential predictor of breeding bird densities.

Key Words

Individuality; Sociality; Birdsong; Lincoln's sparrow; White-crowned sparrow

Introduction

In many situations, individual discrimination within vocalizations can be important to receivers (Blumstein and Munos 2005; Rendall et al. 1996; Stoddard et al. 1991; Weiss et al. 2001) and to signalers (Rendall et al. 1996; Sayigh et al. 1990; Weiss et al. 2001). Individual discriminatability depends on the amount of variation within and among individuals. For a vocalization to have a high degree of individuality, the variation among individuals must exceed the variation within an individual. If individuals within a species exhibit large amounts of variation in their own calls, relative to the variation among individuals, such as seen in male great bitterns, *Botaurus stellaris* (Puglisi and Adamo 2004), then these individuals cannot be discriminated. By contrast, corncrakes, *Crex crex*, can be easily identified using their vocalizations, indicating a relatively low amount of intraindividual variation relative to interindividual variation (Terry and McGregor 2002).

The degree of individuality present within a vocalization can be quantified using the Beecher information statistic (Beecher 1989; Blumstein and Munos 2005; Pollard et al. 2010; Pollard and Blumstein in review). This statistic, derived from information theory, quantifies individuality by yielding a numerical value in bits (Beecher 1989). The higher this value is for a given vocalization, the more individuality present in the vocalization. Thus, high Beecher information statistic values indicate high levels of interindividual variation relative to intraindividual 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 been used to examine the relationship between sociality and individuality. The assumption is that more social species have greater benefits

from producing individually distinctive vocalizations (Beecher 1982; Beecher 1989; Medvin et al. 1993). Indeed, Beecher (1988) discovered that barn swallows, *Hirundo rustica*, and northern rough-winged swallows, *Stelgidopteryx serripennis*, two non-colonial swallow species, exhibit a lower degree of individuality in their parent-offspring recognition vocalizations than bank swallows, *Riparia riparia*, and cliff swallows, *Petrochelidon pyrrhonota*, two colonial species. Pollard and Blumstein (in review) 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). Regardless of the non-breeding season, 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 less dense neighborhoods. This may prove advantageous in discriminating among neighbors and strangers (Baker et al. 1981; Stoddard et al. 1991), subspecies (Petrinovich and Patterson 1981), and dialects (Thompson and Baker 1993), as well as in the responsiveness of females to song (Baker et al. 1987).

The aim of our study was to examine the relationship between density and vocal individuality in two species of sparrows: Lincoln's sparrows, *Melospiza lincolnii*, and mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*. These two species were chosen for two reasons. First, they live in similar habitat, a factor that allows us to discount environmental factors accounting for song structure (Ammon 1995; Chilton et al. 1995). Second, while not congeners, both species are in the family Emberizidae. Thus, we can partially discount the effects of evolutionary history on explaining any observed divergence in vocal individuality.

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, as well as conducted a literature review to examine densities of each species at other sites. We expected that the species living in greater density would have a greater Beecher information statistic.

Methods

Recording and measuring songs

This study was conducted with free-living Lincoln's sparrows and mountain white-crowned sparrows in and around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, U.S.A (38° 57' 46" N 106° 59' 34" W). A single observer walked around the town site and the surrounding area listening for calls made by both species. Each individual was then approached and recorded using a Sennheiser MZW 816 microphone (Sennheiser Electronic, Wedemark, Germany), Dcode PS-T power module (Denecke Inc., North Hollywood, California, U.S.A.), 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 20m due to the varying tolerance of each individual to our approach. We recorded songs from ten males of each species on two separate days, with ten songs recorded during each session. Given that both species were highly territorial, we assumed that recordings made in the same location were from the same bird. To ensure recordings were from the same individuals, each recording location was noted, and recordings were conducted toward the same tree or willow, *Salix spp.*, grove. No recording took place during rain or wind to ensure the highest quality sound.

The sound files were transferred to an HP Pavilion dv6000 computer (Hewlett-Packard Company, Palo Alto, California, U.S.A.) and all 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 (Dynamic range = 40dB) helped us identify possible attributes to measure. We measured twenty-nine variables from each Lincoln's sparrow song and twenty variables for each mountain white-crowned sparrow song. These variables were selected to quantify potential individual variation. For Lincoln's sparrows, we measured (Fig. 1a) the overall minimum and maximum frequency, the minimum and maximum frequency of each note set, the song duration, the number of note sets, the number of notes within each note set, and the duration of each note. For white-crowned sparrow songs, we measured (Fig. 1b) several attributes of the whistle including the total whistle duration, the median frequency of the whistle, the total number of whistle pulses, the number of pulses within each set, and the duration of each whistle pulse. In addition, for white-crowned sparrows, we measured the overall minimum and maximum frequency of each song, the total song duration, the minimum and maximum frequency of each note set, the number of terminal notes, the minimum and maximum frequency of each terminal note, and the duration of each note. We used a principal component analysis in PASW 18 (SPSS Inc. 2010; 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 those that were significant ($p < 0.05$). *F*-values from significant factors were used to calculate the Beecher information statistic (Beecher 1989; Blumstein and Munos 2005; Pollard et al. 2010). Since no statistical test existed to compare Beecher's information statistics, we jackknifed each data set 1,000 times, randomly removing

one F -value each time to test for significance (Hood 2009). We used an independent samples t -test to test for the difference between these two jackknifed data sets.

Point Counts

To examine relative numbers of each species in our study site, one observer walked a transect bisecting the entire study site. Starting from 300m out, the number of individuals heard singing during a 5 minute point count was noted. Following that count, the observer walked 300m and repeated this. A total of 16 censusing points were censused on five separate occasions. We then fitted a general linear model in PASW 18 (SPSS Inc. 2010) to these point count data where species was a fixed effect and censusing point was a random effect.

In addition to censusing our study site, we reviewed the literature and summarized species densities at other sites. We began our literature review by accessing the species account for Lincoln's sparrow (Ammon 1995) and white-crowned sparrow (Chilton et al. 1995). Searches were made for "Lincoln's sparrow territory" and "white-crowned sparrow territory" using Google Scholar (Google 2010). Finally, researchers studying the two species were contacted for information regarding territory size (Ammon 1995; Foufopoulos pers. comm., unpublished data 2010).

Results

We calculated a Beecher's information statistic value of 6.80 bits for Lincoln's sparrows, and 8.76 bits for mountain white-crowned sparrows at our study site. Results from the jackknifed data revealed a significantly ($t = -126.15$, $p < 0.001$) higher degree of individuality contained within the calls of mountain white-crowned sparrows (8.24 ± 0.41) than Lincoln's sparrows (6.54 ± 0.11).

At our study site, there was a significant interaction between the species and the census location ($F_{15, 128}=20.247$, $p<0.001$) for the number of singing male individuals, but there were no significant main effects for either species ($F_{1, 15}=2.499$, $p=0.135$) or location ($F_{15, 15}=0.974$, $p=0.520$) for the number of singing male individuals. The mean number ($\pm$ SD) of Lincoln's sparrows was 2.90 ± 1.83 males/point count while the mean ($\pm$ SD) number of white-crowned sparrows was 2.09 ± 0.90 males/point count.

We obtained three publications reporting territory size in Lincoln's sparrows (Ammon 1995; Speirs and Speirs 1968; Wortman-Wunder 1997) and three reports of territory size in white-crowned sparrows (Foufopoulos pers. comm., unpublished data 2010; Patterson and Petrinovich 1978; Ralph and Pearson 1971). In reviewing the literature, the mean ($\pm$ SD) number of Lincoln's sparrows was 3.63 ± 3.53 pairs/hectare while the mean ($\pm$ SD) number of white-crowned sparrows was 4.97 ± 3.60 pairs/hectare.

Discussion

Taken together, we found preliminary support for the hypothesis that vocal individuality, measured using Beecher's information statistic, covaries with breeding bird density: the more social species was more individualistic. Although our point counts revealed no significant difference in breeding bird densities at our site, a review of the literature suggested that white-crowned sparrows typically live at higher densities than Lincoln's sparrows (Ammon 1995; Foufopoulos pers. comm., unpublished data 2010; Patterson and Petrinovich 1978; Ralph and Pearson 1971; Wortman-Wunder 1997).

White-crowned sparrows'songs contained significantly more individualistic information than Lincoln's sparrows'songs. Indeed, white-crowned sparrows are more social during the non-breeding season too; they form flocks of up to ten individuals (Chilton et al. 1995). By

contrast, when Lincoln's sparrows are not breeding, they are usually alone, but will sometimes form flocks of a few individuals (Ammon 1995). Thus, our results generally support the hypothesis that social density is associated with song individuality.

In summary, while previous work has shown strong associations between sociality and vocal individuality in colonial versus non-colonial birds (Beecher 1988; Medvin and Beecher 1986), and in sciurid rodents (Pollard and Blumstein in review), our study suggests that the relationship between sociality and individuality may extend to breeding bird densities. Clearly, more work needs to be done to examine the extent to which this relationship may hold true. We suggest the possibility of conducting this study with a greater sample size and more extensive point count, and/or the use of other bird species.

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Figure Legends

Fig. 1 A) Spectrogram of a Lincoln's sparrow song showing attributes of the song and variables measured; B) spectrogram of a white-crowned sparrow song showing attributes of the song and variables measured.

Fig. 1

