

Short Communications

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Snow Buntings Sing Individually Distinctive Songs and Show Inter-annual Variation in Song Structure

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ABSTRACT.—Birds use song to communicate with conspecifics, and song can influence both intra-sexual competition and inter-sexual mate choice. Some birds produce repertoires consisting of hundreds of songs while others produce a single song type. For species with a single-song repertoire, there are varying levels of inter-individual variation which can be the result of environmental, genetic, and physiological factors. Male Snow Buntings (*Plectrophenax nivalis*) typically produce a single song type, and while syllable sharing occurs between individuals, many researchers have anecdotally noted the individuality of each male's song. To investigate this long-held assertion, we performed a detailed bioacoustic analysis of male Snow Buntings recorded in the Canadian Arctic. We use canonical discriminant analysis to provide quantitative evidence confirming that male Snow Buntings sing individually distinctive songs. Furthermore, we present the first evidence that some Snow Buntings exhibit inter-annual variation in song structure; while songs remain consistent within each year, two males changed their song type between years. Inter-individual variation in song content can have important behavioral implications, because it facilitates individual recognition and can affect individual fitness. Received 26 September 2013. Accepted 20 January 2014.

Key words: individual distinctiveness, individual recognition, inter-annual variation, *Plectrophenax nivalis*, Snow Bunting, song.

Birds rely heavily on acoustic communication to facilitate survival and reproduction. Songs are generally long, complex vocalizations that birds use for territory defense and mate attraction (Tinbergen 1939, Catchpole and Slater 2008). In

some bird species, each individual produces a repertoire of songs comprised of multiple song types (e.g., *Parus major*; McGregor et al. 1982) although the most common song repertoire size is one (e.g., *Poecile atricapillus*; Horn et al. 1992; MacDougall-Shackleton 1998). In species with a single song type repertoire, there can still be tremendous variation between individuals, where individuals of some species sing nearly identical songs and individuals of other species sing remarkably different songs (Catchpole and Slater 2008).

Snow Buntings (*Plectrophenax nivalis*) are Arctic-breeding passerines which use song for mate attraction and territory defense (Tinbergen 1939, Nethersole-Thompson 1966). Although syllable sharing occurs, each male sings a single song type which has been qualitatively described as individualistic (Tinbergen 1939, Borror 1961, Drury 1961, Nethersole-Thompson 1966, Montgomerie and Lyon 2011). The only quantitative study to date (Espmark 1995) showed higher coefficients of variation in song features between males compared to within males, supporting the idea of individual distinctiveness. In this study, we conducted a detailed bioacoustic analysis of field recordings and used discriminant analysis to determine whether or not individuals could be quantitatively distinguished based on fine structural features of their song. We also recorded birds that returned to the study site across multiple years to describe inter-annual variation. Individual distinctiveness in songs has been demonstrated in other songbird species and can have important inter-sexual and intra-sexual implications.

METHODS

Song Recording and Analysis.—We recorded 19 male Snow Buntings on East Bay (Mitivik) Island, Nunavut, Canada in June and July 2010 and 2011. East Bay Island is covered with loose granite rock which provides ideal nesting habitat

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for Snow Buntings and is likely responsible for the high breeding densities on the island (Guindre-Parker et al. 2013). We used a directional microphone (Sennheiser K6/ME66) and a solid-state digital recorder (Marantz PMD 660; 44,100 Hz sampling rate, 16 bit accuracy, WAVE format). All of the recorded birds were distinguished by unique color band combinations as part of a long-term monitoring project (see Guindre-Parker et al. 2013). In the laboratory, we filtered recordings to remove background noise outside the song range of Snow Buntings (high-pass frequency: 867 Hz; low-pass frequency: 13,939 Hz) and normalized recordings to -3 dB in Audition v. 3.0 (Adobe, San Jose, CA, USA). We then performed detailed measurements of time and frequency features in Avisoft SAS Lab Pro v. 5.2 (R. Sprecht, Berlin, Germany) using the automated parameter measurement tool (temporal resolution: 5.8 ms; frequency resolution: 86 Hz); this approach minimized human measurement error and subjectivity. Syllable counts and syllable typing were determined by visual inspection. We defined “syllables” as elements or clusters of elements that fell into clear groupings, and syllables that looked different from one another were considered to be different types.

We analyzed 10 songs from each male (following from Espmark 1995, 1999; Hofstad et al. 2002), focusing on high quality songs with minimal overlapping non-target sounds. The 10 songs were taken from multiple sessions on different days for each individual (mean \pm SE: 2.68 ± 0.22 recording days/individual; range: 2–5 days). For each individual, the recording sessions were collected on days that ranged from 1–13 days apart (mean \pm SE: 6.05 ± 0.77 days between sessions). For four males, we collected fewer than 10 high quality songs in our focal recordings; for these males we included 1–7 songs recorded by an array of autonomous digital recorders placed across the island (Wildlife Acoustics SM2-GPS; 22,050 Hz sampling rate, 16 bit accuracy, WAVE format; details in Mennill et al. 2012). We ensured these recordings unambiguously originated from the same males as the focal recordings by assessing both the location of the recording and the spectral similarity of the song.

We measured the following structural features from 190 songs: (1) song length (time from start to end of a song, in sec); (2) note duration (sum of

note lengths within a song, in sec; equivalent to duty cycle); (3) total number of syllables; (4) number of unique syllable types; (5) minimum song frequency; (6) maximum song frequency; (7) average minimum syllable frequency (average across all syllables in each song); and (8) average maximum syllable frequency (average across all syllables in each song). All frequency measurements were calculated relative to a threshold of -30 dB below the maximum in AviSoft.

Statistical Analysis.—We conducted a canonical discriminant function analysis to test whether songs could be correctly assigned to the birds that produced them. We ran the discriminant analysis using a cross-validation approach. We randomly selected 75% of the data (i.e., we randomly selected 75% of the data across all males, so that each of the 19 males contributed 6 to 9 songs to the initial stage of analysis) and performed the discriminant analysis on these data. We then tested the accuracy of the discriminant analysis on the remaining 25% of the data (i.e., 1–4 songs from each of the 19 males).

RESULTS

Songs sung by different male Snow Buntings were readily distinguished when viewed as spectrograms by an analyst (Fig. 1). Discriminant analysis of measurements of the fine structural details of songs confirmed that males sing individually-distinctive songs: cross-validation assigned 91.5% of songs to the correct male (41 out of 44 songs in the cross validation dataset), significantly higher than the 5.3% expected by chance for 19 males (i.e., a chance rate of one in 19; binomial test, $P < 0.001$; Fig. 2). Variables that contributed most strongly to the first canonical axis were *average minimum syllable frequency* and *average maximum syllable frequency*, and this axis explained 32% of the variation in males' songs. Variables that contributed most strongly to the second canonical axis were *number of unique syllable types* and *average maximum syllable frequency*, and this axis explained 27% of the variation in males' songs. The 95% confidence ellipse for each male overlapped with the 95% confidence ellipses of 6.1 ± 0.6 other males in the plot of the first canonical versus second canonical axes (Fig. 2), indicating that most males can be distinguished from each other on the basis of just these two canonical axes.

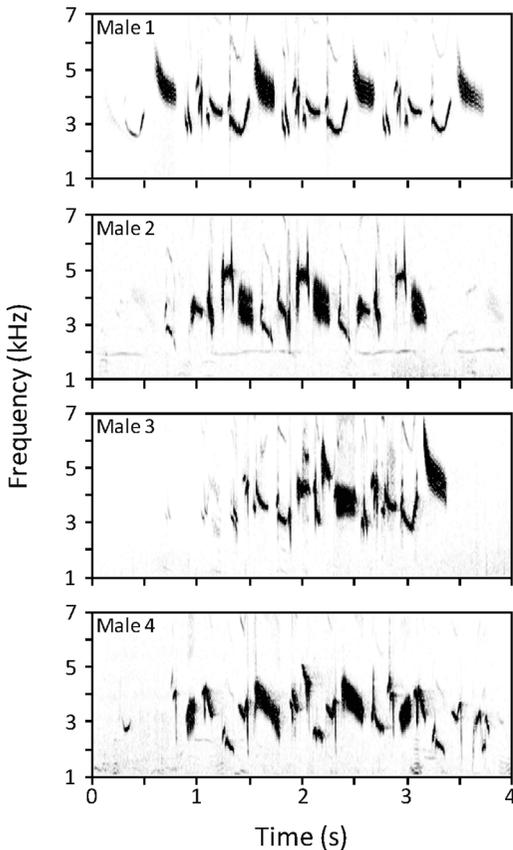


FIG. 1. Sound spectrograms of four example songs of male Snow Buntings recorded on East Bay Island, Nunavut. Songs were analyzed with an automated parameter measurement tool and individual distinctiveness was confirmed with a canonical discriminant analysis. These four songs were chosen to represent typical songs within our study population.

We recorded three males in both 2010 and 2011. We discovered that while most male Snow Buntings produce a single song type within each breeding season, there is inter-annual variation in song structure. Two of the three males we recorded in both 2010 and 2011 sang songs in 2011 which showed striking differences from the previous year (Fig. 3). These birds were neighbors in 2011 and produced songs that were similar to one another in that year.

DISCUSSION

We provide quantitative evidence confirming the long-held assertion that male Snow Buntings sing songs that are individually distinctive. This song feature of Snow Buntings has been reported

anecdotally since the 1930s, based on observations from locations around the world including Scotland, Norway, Greenland, and Canada (Tinbergen 1939, Borror 1961, Drury 1961, Nethersole-Thompson 1966, Espmark 1995, Montgomerie and Lyon 2011). A study of Snow Buntings in Norway revealed significant differences between individuals in song features, and higher coefficients of variation in acoustic features between individuals compared to within individuals (Espmark 1995). We used bioacoustic measurements of songs, including songs from the same males sampled repeatedly on different days, followed by discriminant analysis to demonstrate that songs could be assigned to the correct individuals at levels that exceed chance. The average minimum and maximum syllable frequencies, as well as the number of unique syllable types, were the most important features in these discriminant analyses, suggesting that these may be the most distinctive components of a Snow Bunting's song. Our results are the first to show inter-annual variation in the song structure of Snow Buntings; two of three banded males that were recorded in two separate years sang different songs, whereas one male maintained the same song across years.

Within a species, song often shows significant inter-individual variation. This variation can provide important information to conspecifics, including individual identity. Being able to distinguish between individuals may be beneficial for multiple reasons. For example, individual recognition can play a role in territory defense, with individuals recognizing and habituating to familiar neighbors, decreasing the costs of territory defense against established territorial rivals (Brooks and Falls 1975). Further, female songbirds may discriminate between different males' songs which can have important reproductive implications (Lind et al. 1996, Wiley et al. 2010). Snow Buntings are socially monogamous but genetically promiscuous (Espmark and Moksnes, unpubl. data cited in Hofstad et al. 2002), and individually distinctive songs may allow females to distinguish between social partners and extra-pair partners, for example. Snow Buntings nest within rock crevices, and song recognition may be particularly important for cavity-nesting species since it can facilitate effective intra-pair communication in the absence of visual cues (Lind et al. 1996). This is in line with Nethersole-Thompson's (1966) suggestion

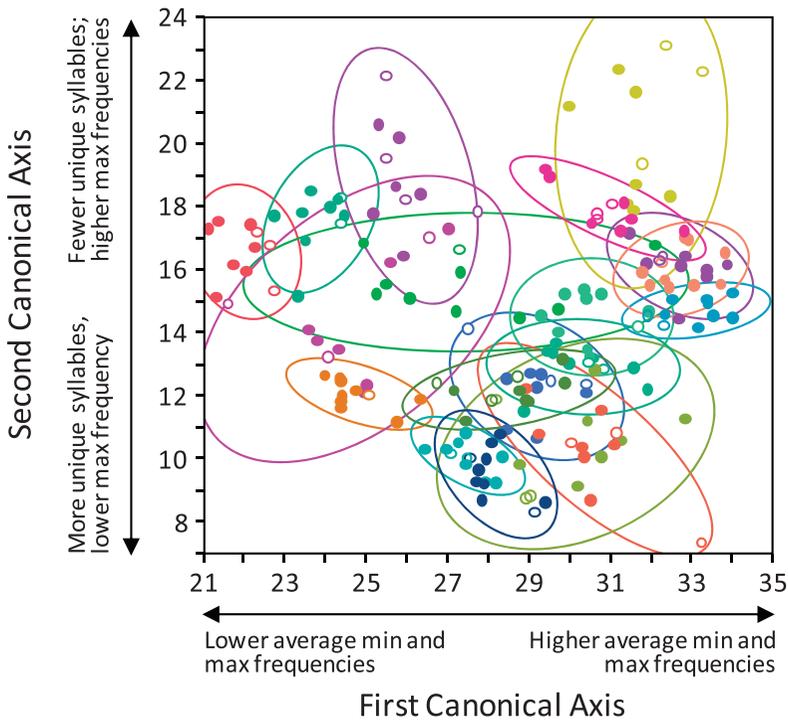


FIG. 2. Plot of the first two canonical axes from discriminant analysis between 19 Snow Buntings on the basis of eight fine structural measurements of males' songs. Each of the 19 males is represented by a different color, and all 10 songs are shown for each male, including the sounds used to construct the discriminant analyses (filled circles) and those used in cross-validation (open circles). 95% confidence ellipses around the multivariate mean for each male are shown.

that males may use song to call brooding females off their nests. Additionally, individual recognition may be important for parent-offspring contact; fledged Snow Bunting chicks seemingly recognize and respond to their father's song (Nethersole-Thompson 1966; SB, pers. obs.).

To the best of our knowledge, inter-annual variation in song structure has never been reported in Snow Buntings. We recorded three birds in 2010 and 2011 and found that two of them changed their song between years. Interestingly, in 2011 two of these individuals were neighbors and produced similar songs to one another (Fig. 2). There are two suggested processes behind song sharing: instructive learning and selective-based learning (Nelson and Marler 1994). Instructive learning suggests that song sharing results from birds learning the local dialect or song(s) of their neighbors as young birds or upon settling on new territories. Selective learning suggests birds learn a variety of song types and then retain and produce a subset of songs that best match neighbors' songs or the local dialect (Nelson and Marler 1994). We

suggest that males may learn a variety of syllables, or full songs, and hone in on one song type at the start of each year, possibly to match the songs of nearby local males. This is in line with the observation that neighbors' songs were occasionally nearly identical, with high syllable sharing, on Svalbard (Espmark 1999), and that local dialects occurred in Greenland (Tinbergen 1939) and the Canadian Arctic (Montgomerie and Lyon 2011). White-crowned Sparrows (*Zonotrichia leucophrys*), like most Snow Buntings, produce a single song type as adults, but often over-produce multiple songs at the start of their first breeding season before selecting one song (Hough et al. 2000). A similar process may occur annually in Snow Buntings.

At least three areas are important for future research on Snow Bunting song: (1) Although we have demonstrated that songs contain individually distinctive features, playback studies will be required to confirm that Snow Buntings use this information to distinguish between individuals, possibly using neighbor-stranger discrimination experiments (as in Brooks and Falls 1975, for

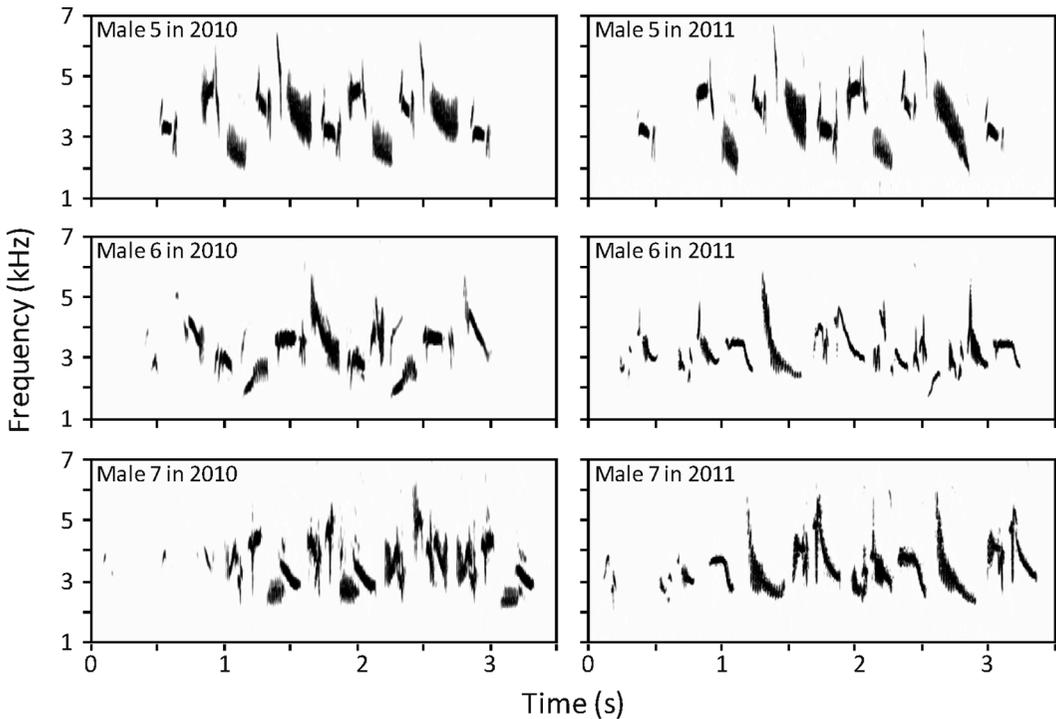


FIG. 3. Within a breeding season, a male Snow Bunting sings a single individually distinctive song. However, between-year recordings of three color-banded males reveal that two males (Male 6 and Male 7) showed inter-annual variation in song structure.

example). (2) Tinbergen (1939) studied Snow Buntings in Greenland and noted that neighbors' songs can sometimes sound nearly identical. In 2011, we encountered a pair of neighboring males singing highly similar songs (Male 6 and 7; Fig. 3), although our discriminant analysis confused the males in these pairs rarely (only 1 of 20 songs was misclassified as the neighbor). Further studies should investigate how often adjacent territorial males produce similar songs and whether this phenomenon has social consequences for territorial dynamics. (3) Longitudinal studies should be performed to further examine the similarity of a male's song across years. Future studies that follow the same individuals over multiple years may further our understanding of the factors affecting song learning, the proximate role of song in Snow Buntings, and the degree of intra-male song flexibility in this species.

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Hybridization of a Lesser Black-backed Gull and Herring Gulls in Eastern North America

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ABSTRACT.—We present the first confirmed case of hybridization between a Lesser Black-backed Gull (*Larus fuscus*) and Herring Gulls (*Larus argentatus*) in North America (outside of Greenland). We discovered a Lesser Black-backed Gull × Herring Gull pair on Appledore Island, Maine in 2007. Nuclear DNA analysis indicated that the Lesser Black-backed Gull was the genetic parent of the chicks from 2008 to 2011. The offspring have not returned to breed, so we do not know if they are fertile. Increasing numbers of observations of Lesser Black-backed Gulls, including putative Lesser Black-backed Gull × Herring Gull hybrids along the Atlantic coast, indicate that Lesser Black-backed Gulls may be in the process of colonizing

North America. If so, additional hybridization with Herring Gulls is likely in areas of overlap. *Received 11 June 2013. Accepted 13 February 2014.*

Key words: avian hybridization, Gulf of Maine, large white-headed gulls, *Larus argentatus*, *Larus fuscus*, range expansion.

Lesser Black-backed Gulls (*Larus fuscus*, Linnaeus, 1758) breed primarily in northern and western Europe and have undergone a significant range expansion north and west as well as south during the past century (Cramp and Simmons 1983, Calladine 2004, Boertmann 2008). The species colonized Iceland between 1920–1930 and Greenland between 1986–1990. They also colonized the Netherlands, Germany, Spain, Portugal, and recently expanded to the Canary Islands (Cramp and Simmons 1983, Grande and Palacios 2002). This expansion mainly involved the subspecies *graellsii* (Post and Lewis 1995).

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