

Male song individuality over female breeding periods in Savannah sparrows (*Passerculus sandwichensis*)

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Abstract

Song individuality in songbirds is a prerequisite for individual recognition, which plays an important role in communication between pair members, relatives, or neighbors. We investigated song individuality of Savannah sparrow (*Passerculus sandwichensis*) males over a single breeding season. We recorded songs from 11 color-banded males during each of the four female breeding periods (pre-pairing, pairing and egg-laying, incubation, and nestling and fledging). We analyzed 10 songs from each male, with 13 temporal and nine frequency variables that represented the structural characteristics of songs to examine individual variation throughout the breeding season. The results of nested analysis of variance (ANOVA) showed that all song variables differed among individuals across breeding periods and among breeding periods across individual songs except for F9 (peak frequency difference between the first and the second trill parts). A discriminant function analysis showed that songs of pre-pairing periods were clearly separated from those of the other periods. These results suggest that the songs of males display individuality and maintain potential information about his mating status and his mate's reproductive condition across the breeding season.

Key words

Bird song, breeding period, individuality, *Passerculus sandwichensis*, seasonal variation.

Introduction

Many bird species display vocal individuality (individually specific vocalizations) that provides potential information about the signaler (BECKER, 1982; FALLS, 1982; MILLER 1983; 1996). They can discriminate between members of breeding pairs, relatives, and neighboring males through their vocalizations (WILEY & WILEY, 1977; COLGAN, 1983; BEECHER, 1988; 1989; YDENBERG *et al.*, 1988; PRICE, 1999). Songs as vocal signals in songbirds (Passeriformes: Oscines) may provide various benefits through song individuality especially when visual communication is limited, such as in nocturnal birds and birds in tall grass meadows and dense forests (REK & OSIEJUK, 2010; NAGY & ROCKWELL, 2012; YEE *et al.*, 2016). In addition, neighboring males may save time and energy from minimizing territorial competition between familiar individuals (STODDARD *et al.*, 1991).

Song individuality is a prerequisite for individual recognition in birds by voice. Individual recognition is largely dependent upon their within- and/or between-song stereotypy within individuals and the songs vary between individuals (FALLS, 1982; WEARY *et al.*, 1990). In addition, the signal for individuality is not only limited to vocalization, but also applies to instrumental sounds (BUDKA *et al.*, 2018). Such signals may contain certain cues (e.g., a distance cue in male-male territorial competitions), minimizing the chance for confusion by the receiver in the social communication system, where the signals should efficiently convey information to receivers and provide accurate information about the singer's location, identity, and quality (ENDLER, 1993; CHRISTLE *et al.*, 2004; DuBois *et al.*, 2011).

Song has two main functions in male songbirds: territoriality and mate attraction functions (CATCHPOLE & SLATER, 2008). Males producing songs indicative of high-quality males, such as higher complexity, faster rate of songs, and more song types, may achieve better reproductive performance, while females responding appropriately to the males may increase their reproductive fitness directly or indirectly (BALSBY, 2000; CATCHPOLE & SLATER, 2008; IRSCHICK *et al.*, 2015). As a result, song has been a primary target of sexual selection. Many studies have examined differences in the structure and usage of male songs between paired and unpaired males (HENNIN *et al.*, 2009), between female fertile and non-fertile periods (BALLENTINE *et al.*, 2003), and between breeding and non-breeding seasons (LEITNER *et al.*, 2001; HILL *et al.*, 2015). Although some males that use songs primarily to attract a female rapidly decrease singing after pairing, they continue to produce songs in various situations regarding intra- and inter-sexual communication (e.g., Savannah sparrows, *Passerculus sandwichensis*, BÉDARD & LAPOINTE, 1984; SUNG, 2004), which suggests that the song structure and usage by the birds contribute to the individual's identity during the breeding periods in the context of intra- and inter-sexual communication.

Here, we describe and analyze, for the first time, songs of the Savannah sparrows according to female breeding periods. These birds are widespread across most of North America. They are sexually monomorphic in plumage and are socially monogamous in this study area (WHEELWRIGHT & RISING, 1993). They lay eggs on the ground. The songs of each male typically show one song type with minor variation in the number of introductory syllables or the length of a trill section (BRADLEY, 1994). Till now, the songs of Savannah sparrows have been studied by several authors focusing mainly on geographic song variation within and among populations (BRADLEY, 1977; CHEW, 1981; PITOCHELLI, 1981; BURNELL, 1998) and cultural evolution (WILLIAMS *et al.*, 2013). In particular, WILLIAMS *et al.* (2013) suggested that song segments within the song convey different information, where the middle segment may serve to denote individuality, while the terminal trill duration and the number of clicks in the introduction segment are under selection. Thus, we can expect that song structural features for individual identity may exist during the female breeding periods, and that the songs of unpaired males during the pre-pairing period may differ from those of other periods in certain song characteristics to attract female receivers as well as to compete with neighbors.

Material and methods

This study was conducted in grasslands along forest margins at A'Nowaghi Forest Ponds, located approximately 10 km south of the city center of London, Ontario, Canada, in 2001. Most of the males were captured with mist nets and banded with a standard Canadian Wildlife

Service aluminum band in addition to a unique combination of either one or two color bands to allow individual recognition. Individual territories were determined, numbered, and mapped on aerial photographs through daily observation of activities (e.g., use of song perches, locations of aggressive encounters, and foraging).

The field work was carried out from 15 April to 22 July 2001. Daily observations and song recordings for each male were primarily made in the early morning (sunrise to 11:00 hours) and infrequently in the afternoon (11:00 hours to 17:00 hours) and evening (17:00 hours to sunset) due to low singing activities at this time. Observations were performed in each nest over a 10-minute period within approximately 2 meters of each territorial boundary after checking whether the subjects had been disturbed or not. Time, location, nest stage, and behavioral observations were recorded at each nest. To examine variation in song structure according to female breeding periods, the breeding period was divided into the following four stages: (1) pre-pairing (the period from territory settlement to just before female arrival), (2) pairing (the period from the first day of female arrival to just before the first egg is laid) and egg-laying (the period between the first and last egg-laying time points), (3) incubation (the period from the last egg-laying time point to the period when the first egg hatches), and (4) nestling (the period from the first day of egg-hatching to just before fledging starts) and fledging (the period after the chicks leave the nest) periods. Observations and song recordings started in a randomly chosen order. For observations, 10 × binoculars and a 20 × spotting scope were used. Recordings were made using a Sony PMD222 tape recorder and a Telinga parabolic microphone.

Song analyses were carried out using Canary 1.2 (Cornell Laboratory of Ornithology, 1995). Ten good quality songs (i.e., with low background noise) were randomly selected from each of the 11 males during each of the four breeding periods. We partitioned the songs into seven sections depending on a recognizable sequence in a song (Fig. 1). These sections included series of repeated similar syllables (Sections I and II); complex syllables (Sections III and V); trills (Sections IV and VI); and terminal buzz (Section VII). Thirteen temporal and nine frequency variables (Fig. 2) of each song that represented the structural characteristics in each section of the song were selected and measured from oscillograms and spectrograms with a filter bandwidth of 699.40 Hz and frame length of 128 points produced using a Hamming window.

All data were analyzed using the means of individuals during different breeding periods. Normality assumptions of the data were tested with a One-Sample Kolmogorov-Smirnov Test ($P > 0.05$). If assumptions were not met, the data were transformed appropriately (ZAR, 1999). Means and coefficient of variation (CV; the ratio of the standard deviation to the mean) were calculated for each variable across breeding periods. Nested analysis of variance (ANOVA) was used to 1) test differences among and within individuals across breeding periods within the year of 2001 and 2) estimate variance compo-

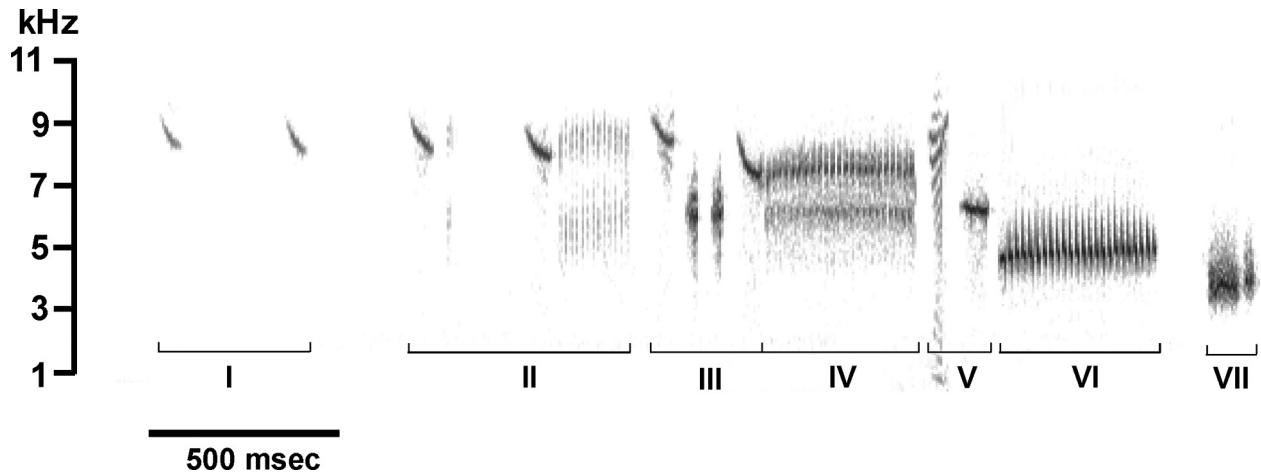


Fig. 1. Example of Savannah sparrow song subdivided into seven sections I–VII.

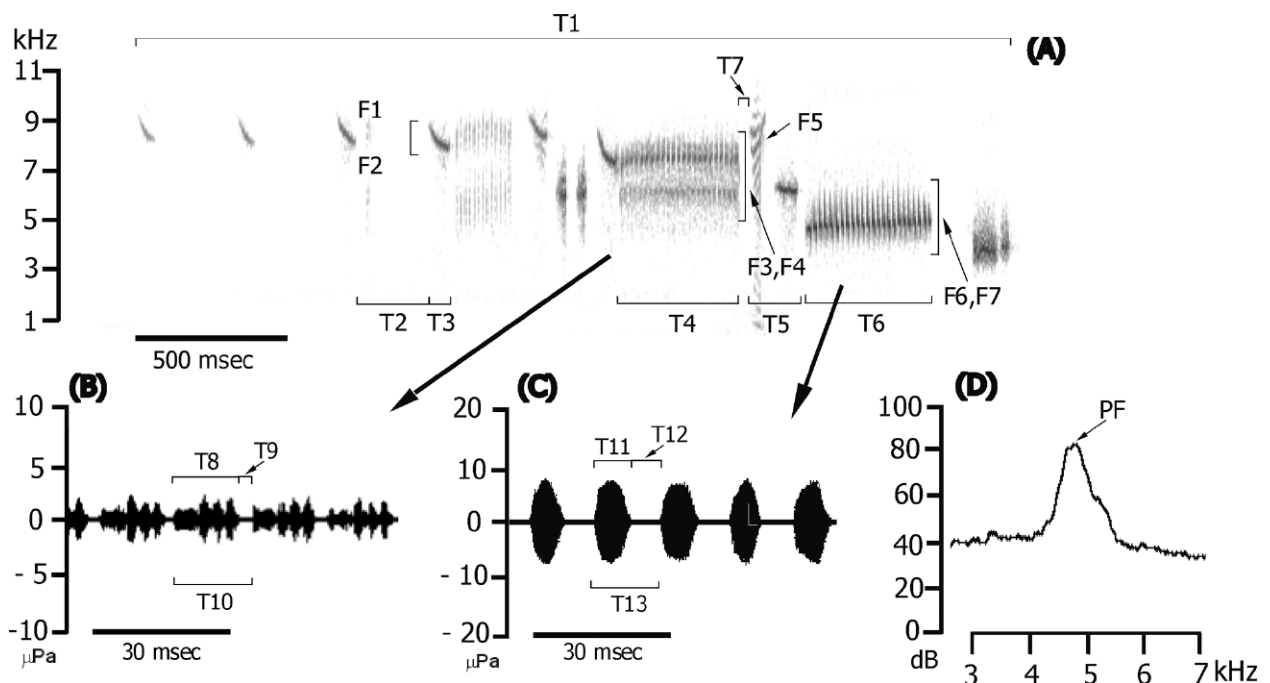


Fig. 2. The acoustic variables used in the study. (A) T1 (song duration); T2 (interval between the first and the third syllables of section II); T3 (duration of the third syllable of section II); T4 (duration of section IV); T5 (duration of section V); T6 (duration of section VI); T7 (interval between section IV and section V); F1 (maximum frequency of the third syllable of section II); F2 (minimum frequency of the third syllable of section II); F3 (peak frequency of section IV); F4 (bandwidth of section IV); F5 (peak frequency of first syllable of section V); F6 (peak frequency of section VI); F7 (bandwidth of section VI); F8 (bandwidth of entire song); F9 (F3 minus F6). (B) T8 (element duration in section IV); T9 (interval between two elements in section IV); T10 (T8 plus T9). (C) T11 (element duration in section VI); T12 (interval between two elements of section VI); T13 (T11 plus T12). (D) PF (peak frequency), for which we used power spectrums to measure each F3 of section IV and F6 of section VI.

nents attributable to song variation within breeding periods (MS_B/MS_S) and songs of breeding periods within males (MS_I/MS_B). Discriminant function (DF) analysis was performed to reveal differences in song features among breeding periods, and the first two DF scores were plotted. One-way ANOVA was used to test the effects of breeding periods on the song features, while Student-Newman-Keuls (S-N-K) was used for post-hoc tests.

Results

Many song features showed higher levels of variation during the incubation period, but significant differences were not detected among breeding periods when all individuals were considered ($F_{3, 84} = 0.261$, $P = 0.854$, Table S1). Except for one temporal (T10) and four frequency (F1, F2, F5, F6) variables, coefficients of variables (CVs)

Table 1. Results of nested analysis of variance for each variable (songs among and within individuals across breeding periods in 2001). MS = mean square; I = individual; B = breeding period; S = song. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Variable	Percent of variance				
	MS _I /MS _B	MS _B /MS _S	Individual	Breeding period	Song
Frequency attributes					
F1	2.60*	13.93***	19.6	45.4	35.1
F2	6.17***	10.35***	40.9	28.6	30.6
F3	38.89***	1.81**	61.3	2.9	35.8
F4	12.11***	6.76***	54.4	16.7	28.9
F5	15.61***	5.58***	58.3	13.1	28.6
F6	46.73***	5.89***	81.6	6.0	12.1
F7	13.55***	4.78***	52.1	13.1	34.8
F8	4.62***	10.90***	33.1	33.3	33.6
F9	32.78***	1.44	52.3	2.0	45.8
Temporal attributes					
T1	3.02**	8.84***	20.1	35.2	44.8
T2	22.30***	4.80***	61.9	11.8	26.3
T3	5.56***	6.215***	31.8	23.4	44.9
T4	11.01***	11.32***	58.2	21.2	20.6
T5	31.74***	6.09***	75.6	8.2	16.2
T6	5.30***	4.43***	26.2	18.9	55.0
T7	22.43***	4.80***	38.6	15.8	45.7
T8	6.04***	5.58***	51.6	33.7	14.8
T9	2.27*	3.99***	20.9	49.5	29.5
T10	26.56***	3.04***	77.8	8.2	14.0
T11	6.69***	6.00***	52.1	30.5	17.4
T12	4.78***	27.50***	47.9	48.8	3.3
T13	7.59***	34.01***	61.1	36.0	2.9

of the yearly average values were greater than 10%, and three variables (F9, T9, T12) showed particularly high variability (> 30%). The songs varied little within each individual but varied greatly among individuals across the breeding periods for all variables (Table 1). The between-male component of variance ranged from 20–82%, where the degree of variance were higher in order of F6 (peak frequency of section VI; 81.6%), T10 (77.8%), T5 (75.6%), T2 (61.9%), and T13 (61.1%). All variables except for F9 (calculated by subtracting F3 and F6) showed significant variation among breeding periods across individual songs; the component of variation ranged from 2–50% across variables in the nested ANOVAs, where the highest variation appeared in T9 (49.5%), T12 (48.8), and F1 (45.4%), respectively. In particular, T12 showed high variation among breeding periods as well as among individuals.

A discriminant function analysis (DFA) classified 84.1% of the songs of the 11 males into their correct breeding periods. DF1 and DF2 explained 71.5% and 20.3% of the total variance, respectively, and DF3 accounted for only 8.2% of the variation. DF1 was negatively correlated with two frequency (F1 and F8) variables and one temporal (T1) variable and positively correlated with T13, while F1 was the most important discriminating variable (Table 2). T11 and T9 also played important roles in the discrimination of DF2 and DF3,

respectively. When DF scores of songs of the 11 males in the four breeding periods were plotted on the first two discriminant functions, the songs of the pre-pairing period were clearly separated from those of other periods by DF1 (Fig. 3). There were significant differences in DF1 scores among the four breeding periods ($F_{3, 40} = 47.369$, $P < 0.001$), and the average score was significantly lower in the pre-pairing period than in any other period (post-hoc test; S-N-K). In addition, DF2 separated the pairing and egg-laying periods from the other periods, with significant differences observed among the four breeding periods ($F_{3, 40} = 13.479$, $P < 0.001$). The average of the periods was significantly lower than that of any other periods (post-hoc test; S-N-K).

Discussion

The songs of Savannah sparrows consistently differed among individual males for all nine frequency and 13 temporal variables, which suggests the potential existence and maintenance of individuality in songs of this bird population across the breeding periods. In particular, F6 (peak frequency of the second trill part of songs), T10 (element duration plus interval between two elements of the first trill part), and T5 (duration between the first

Table 2. Structure matrix from discriminant function analysis of 22 variables of songs of 11 male Savannah sparrows. Discriminating variables are ordered by absolute size of correlation within Function 1, then Function 2, and then Function 3. The variables with highest loadings in each function are shown in bold values. * Largest absolute correlation between each variable and any discriminant function.

Variable	Discriminant function		
	1	2	3
F1	-0.297*	0.084	0.236
F8	-0.231*	0.139	0.077
T1	-0.183*	0.085	-0.120
T13	0.068*	-0.023	-0.022
T11	-0.101	0.252*	-0.036
T2	0.067	-0.110*	-0.105
T12	-0.003	-0.089*	0.061
F9	-0.023	-0.080*	-0.060
F5	0.016	-0.079*	0.007
F3	-0.029	-0.064*	0.023
T10	-0.029	-0.042*	-0.008
T9	0.179	0.073	0.280*
F2	0.007	-0.042	0.274*
T7	0.150	-0.034	-0.270*
T8	-0.150	-0.094	-0.194*
T3	-0.145	0.035	0.149*
T6	-0.136	-0.110	-0.143*
F6	-0.015	0.008	0.120*
T4	-0.078	0.054	0.115*
F4	0.015	-0.023	0.087*
F7	-0.014	0.005	-0.064*
T5	-0.021	-0.041	0.057*
Eigenvalue	3.553	1.011	0.406
Explained variance (%)	71.5	20.3	8.2

and second trill parts) exhibited the greatest variance between the males. These frequency and temporal features as parts of section IV (trill), V, and VI (trill) of the songs suggest an important role for individual identity. However, WILLIAMS *et al.* (2013) suggested that section VI (trill) significantly plays a role in directional cultural selection. Moreover, in a recent study, WILLIAMS *et al.* (2019) suggested that section IV (trill) is a population marker and showed the differences between populations of Kent Island and Williamstown Savannah sparrow songs in pulse periods (T8 in our work) and mean frequency (F3). In our study, these two variables showed relatively high individual variation (Table 2). In addition, geographic variation in surrounding areas including this population showed that the syllables in section II were good candidates to classify populations (SUNG & HANDFORD, 2006). As the possibility of the section IV being simultaneously used as individual as well as population markers is low, further detailed study is necessary at various geographic scales of individuals within and among populations. Song individuality in frequency features in other species has been observed when examined without seasonal

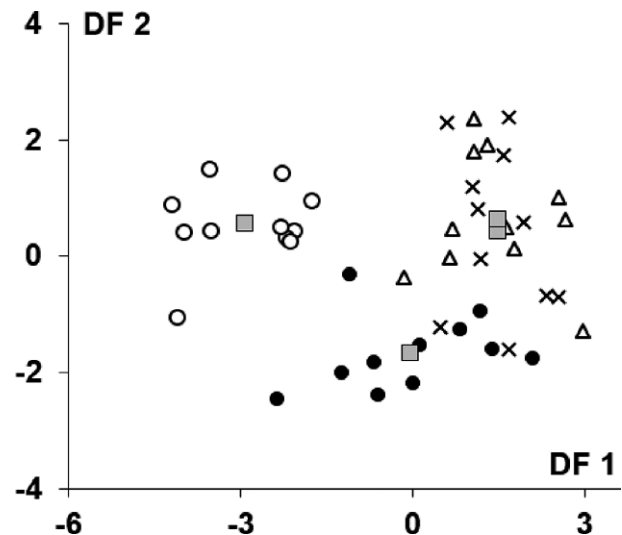


Fig. 3. Plot of the group centroids of 11 individuals along the first two discriminant function axes based on temporal and frequency song variables. P – Pre-pairing period; P + E – Pairing and Egg-laying periods; I – Incubation period; N + F – Nestling and Fledging periods. ○: P; ●: P+E; ×: I; △: N+F; □: Group Centroid.

variation (field sparrow, *Spizella pusilla*, NELSON, 1989; black-capped chickadee, *Poecile atricapillus*, CHARRIER *et al.*, 2004) and in both frequency and temporal features (Acadian flycatcher, *Empidonax vireescens*, WILEY, 2005).

The songs of pre-pairing period were clearly separated from those of the other periods based on DFA results. The songs of the pre-pairing period were assigned to the correct period with 100% accuracy, and the accuracy decreased after this period. In general, Savannah sparrows have only one song type and share many features among males. In addition, each male displays little variation in the number of introductory syllables or the length of a trill part. Nevertheless, such an accurate discrimination of songs of the pre-pairing period from those of the other periods with individual distinctiveness has behavioral significance in three ways. First, as the song is used primarily to attract a mate, structural features of songs may reflect male inter-sexual communication because the songs are uttered by unpaired males. In our study, during the pre-pairing period, males tend to have longer (T1) and more broad-banded (F8) songs with faster trills (T13) compared to other periods of the breeding season. Increased song duration has been used as a reliable signal of male quality in many species because longer songs are more energy costly to produce (LAMBRECHTS & DHONDT, 1987; NOLAN & HILL, 2004), while faster trill rate is one of the main factors that limit the utterance of honest song with narrow frequency bandwidths (PODOS, 1997; PHILLIPS & DERRYBERRY, 2017). In particular, section VI (trill) appeared as an important variable for song individuality (T12) and song quality (T13). Similarly, WILLIAMS *et al.* (2013) suggested the evolutionary role of shorter trills under sexual selection as well as in conveying information about individual identity. Second, while advertising their existence or male quality by emitting consistently

large numbers of songs before pairing (SUNG, 2004), the males may overcome environmental constraints on sound transmission in open habitats. The patterns of song features, including F1, F8, T1, and T13 (T11 + T12), may aid in long-distance communication predicted by the Acoustic Adaptation Hypothesis or AAH (WILEY & RICHARDS, 1982; ROTHSTEIN & FLEISCHER, 1987; BROWN & HANDFORD, 2000). The AAH predicts that long-distance signal will be adjusted in order to maximize transmission efficiency by minimizing signal attenuation and degradation. Song with higher frequencies (F1), broader bandwidths (F8), higher frequency modulations (trills), shorter elements and inter-element intervals (T13) could be adapted in habitats with grass field (MORTON, 1975). Third, distinctive song structures of the pre-pairing period may aid in the recognition of individual neighbors because males continue to compete to occupy and defend a territory after arriving at future breeding sites. Neighboring males could reduce aggression to familiar individuals for further territorial interactions as a result of the “dear enemy” effect (GODARD, 1991; STODDARD *et al.*, 1991; MOSER-PURDY *et al.*, 2017). Territorial male Savannah sparrows also discriminated between neighbor and stranger songs (SUNG, 2004), which indicates that territorial neighbors can reduce unnecessary competition by recognizing neighbors’ songs (FALLS, 1982).

During pairing and egg-laying periods, the males may change from long to short distance communication because of the primary need of contacting their mates over short distances. T11 (element duration) and T12 (interval between two elements) of section VI (trill) were involved in DF2, where trill rate and consistency decreased with decreasing T11 and increasing T12. If the trill section is associated with song individuality and reproductive success (WILLIAMS *et al.*, 2013), it would be especially important for the male to send exact distance cues to attract the female receiver by increasing song consistency. However, the song features appeared to be the opposite.

In conclusion, our results suggest that Savannah sparrows produce songs that potentially play a role in individual identity and that are indicative of high-quality males to attract female receivers and competing with neighbors. The frequency and temporal features as parts of section IV (trill), V, and VI (trill) of the songs played a role for individual identity. In particular, the songs of pre-pairing periods were clearly separated from songs of the other periods. The distinctive songs of the pre-pairing period may aid in male intra- and inter-sexual communication in open habitats; section VI (trill) appeared to play an important role for both song individuality and song quality, which is consistent with the findings of WILLIAMS *et al.* (2013). Further field studies with playback experiments are necessary to investigate whether the trends of song features of individuality are consistent at various geographic scales of individuals within and among populations and to examine which variables the receivers actually use for individual recognition and are associated with reproductive success.

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References

- BALLENTINE, B., BADYAEV, A. & HILL, G. E. (2003). Changes in song complexity correspond to periods of female fertility in Blue Grosbeaks (*Guiraca caerulea*). *Ethology*, **109**, 55–66.
- BALSBY, T. J. S. (2000). Song activity and variability in relation to male quality and female choice in whitethroats *Sylvia communis*. *Journal of Avian Biology*, **31**, 56–62.
- BECKER, P. H. (1982). The coding of species-specific characteristics in birds sounds, pp. 213–252 in: KROODSMA, D. E. & MILLER, E. H. (eds) *Acoustic Communication in Birds*. Vol. 1. New York, Academic Press.
- BÉDARD J. & LAPOINTE, G. (1984). The Savannah Sparrow territorial system: can habitat features be related to breeding success? *Canadian Journal of Zoology*, **62**, 18 19-1828.
- BEECHER, M. D. (1988). Kin recognition in birds. *Behavior Genetics*, **18**, 465–482.
- BEECHER, M. D. (1989). Signalling systems for individual recognition: an information theory approach. *Animal Behaviour*, **38**, 248–261.
- BRADLEY, R. A. (1977). Geographic variation in the song of Belding’s Savannah Sparrow (*Passerculus sandwichensis beldingi*). *Bulletin of the Southern California Academy of Sciences*, **22**, 57–100.
- BRADLEY, R. A. (1994). Cultural change and geographic variation in the songs of the Belding’s Savannah Sparrow (*Passerculus sandwichensis beldingi*). *Bulletin of the Southern California Academy of Sciences*, **93**, 91–109.
- BROWN, T. J. & HANDFORD, P. (2000). Sound design for vocalizations: quality in the woods, consistency in the fields. *Condor*, **102**, 81–92.
- BUDKA, M., DEONIZIAK, K., TUMIEL, T. & WOŻNA, J. T. (2018). Vocal individuality in drumming in great spotted woodpecker – A biological perspective and implications for conservation. *PLoS ONE*, **13**, e0191716.
- BURNELL, K. (1998). Cultural variation in Savannah Sparrow, *Passerculus sandwichensis*, songs: an analysis using the meme concept. *Animal Behaviour*, **56**, 995–1003.
- CHARRIER, I., BLOOMFIELD, L. L. & STURDY, C. B. (2004). Note types and coding in parid vocalizations. I: The chick-a-dee call of the black-capped chickadee (*Poecile atricapillus*). *Canadian Journal of Zoology*, **82**, 769–779.
- CATCHPOLE, C. K. & SLATER, P. J. B. (2008). *Bird song. Biological themes and variations* (2nd ed.). Oxford, Cambridge University Press.
- CHEW, L. (1981). Geographic and individual variation in the morphology and sequential organization of the song of the Savan-

- nah Sparrow (*Passerculus sandwichensis*). *Canadian Journal of Zoology*, **59**, 702–713.
- CHRISTLE, P. J., MENNILL, D. J. & RATCLIFFE, L. M. (2004). Chickadee song structure is individually distinctive over long broadcast distances. *Behaviour*, **141**, 101–124.
- COLGAN, P. (1983). *Comparative social recognition*. New York, John Wiley and Sons.
- DUBOIS, A. L., NOWICKI, S. & SEARCY, W. A. (2011). Discrimination of vocal performance by male swamp sparrows. *Behavioral Ecology and Sociobiology*, **65**, 717–726.
- ENDLER, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical transactions of the Royal Society B: biological sciences*, **340**, 215–225.
- FALLS, J. B. (1982). Individual recognition by sound in birds, pp. 237–278 in: KROODSMA, D. E. & MILLER, E. H. (eds) *Acoustic Communication in Birds*. Vol. 2. New York, Academic Press.
- GODARD, R. (1991). Long-term memory of individual neighbours in a migratory songbird. *Nature*, **350**, 228–229.
- HENNIN, H. L., BARKER, N. K. S., BRADLEY, D. W. & MENNILL, D. J. (2009). Bachelor and paired male rufous-and-white wrens use different singing strategies. *Behavioral Ecology and Sociobiology*, **64**, 151–159.
- HILL, S. D., AMIOT, C., LUBBROOK, M. R. & JI, W. (2015). Seasonal variation in the song structure of tui (*Prosthemadera novaeseelandiae*). *New Zealand Journal of Ecology*, **39**, 110–115.
- IRSCHICK, D. J., BRIFFA, M. & PODO, J. (2015). *Animal Signaling and Function: An Integrative Approach*. Hoboken (NJ), Wiley-Blackwell Press.
- LAMBRECHTS, M. & DHONDT, A. A. (1987). Male quality, reproduction, and survival in the Great Tit (*Parus major*). *Behavioral Ecology and Sociobiology*, **19**, 57–63.
- LEITNER, S., VOIGT, C. & GAHR, M. (2001). Seasonal changes in the song pattern of the non-domesticated island canary (*Serinus canaria*), a field study. *Behaviour*, **138**, 885–904.
- MILLER, E. H. (1983). The structure of aerial displays in three species of Calidridinae (Scolopacidae). *Auk*, **100**, 440–451.
- MILLER, E. H. (1996). Acoustic differentiation and speciation in shorebirds, pp. 241–256 in: KROODSMA, D. E. & MILLER, E. H. (eds) *Ecology and evolution of acoustic communication in birds*. Ithaca (New York), Cornell University Press.
- MORTON, E. S. (1975). Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.
- MOSER-PURDY, C., MACDOUGALL-SHACKLETON, E. A. & MENNILL, D. J. (2017). Enemies aren't always dear: male song sparrows adjust dear enemy effect expression in response to female fertility. *Animal Behaviour*, **126**, 17–22.
- NAGY, C. M. & ROCKWELL, R. F. (2012). Identification of individual Eastern Screech-Owls *Megascops asio* via vocalization analysis. *Bioacoustics*, **21**, 127–140.
- NELSON, D. A. (1989). Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*). *Journal of Comparative Psychology*, **103**, 171–176.
- NOLAN, P. M. & HILL, G. E. (2004). Female choice for song characteristics in the house finch. *Animal Behaviour*, **67**, 403–410.
- PHILLIPS, J. N. & DERRYBERRY, E. P. (2017). Vocal performance is a salient signal for male-male competition in white-crowned sparrows. *Auk*, **134**, 1–11.
- PITOCHELLI, J. (1981). *Song dialects and vocal development of Savannah Sparrows (Passerculus sandwichensis labradorius Howe) breeding in Newfoundland and the St. Pierre et Miquelon Islands*. M.Sc. Thesis. Memorial University of Newfoundland (St. John's).
- PODO, J. (1997). A performance constraint on the evolution of trilled vocalization in a songbird family (Passeriformes: Emberizidae). *Evolution*, **51**, 537–551.
- PRICE, J. J. (1999). Recognition of family-specific calls in Stripe-backed Wrens. *Animal Behaviour*, **57**, 483–492.
- REK, P. & OSIEJUK, T. S. (2010). Sophistication and simplicity: conventional communication in a rudimentary system. *Behavioral Ecology*, **21**, 1203–1210.
- ROTHSTEIN, S. I. & FLEISCHER, R. C. (1987). Vocal dialects and their possible relation to honest status signaling in the Brown-headed Cowbird. *Condor*, **89**, 1–23.
- STODDARD, P. K., BEECHER, M. D., HORNING, C. L. & CAMPBELL, S. E. (1991). Recognition of individual neighbors by song in the Song Sparrow, a bird with song repertoires. *Behavioral Ecology and Sociobiology*, **29**, 211–215.
- SUNG, H. C. (2004). *Song Variation and male reproductive success in the Savannah Sparrow songs, Passerculus sandwichensis*, pp. 1–186. Ph. D. Thesis. University of Western Ontario (London).
- SUNG, H. C. & HANDFORD, P. (2006). Songs of the Savannah sparrow: structure and geographic variation. *Canadian Journal of Zoology*, **84**, 1637–1646.
- WEARY, D. M., NORRIS, K. J. & FALLS, J. B. (1990). Song features birds use to identify individuals. *Auk*, **107**, 623–625.
- WHEELWRIGHT, N. T. & RISING, J. D. (1993). *Savannah Sparrow (Passerculus sandwichensis)*, pp. 1–28 in: POOLE, A., STETTENHEIM, P. & GILL, F. (eds) *The Birds of North America*. No. 45. Washington, American Ornithologists' Union.
- WILEY, R. H. & WILEY, M. S. (1977). Recognition of neighbors' duets by stripe-backed wrens, *Campylorhynchus nuchalis*. *Behaviour*, **62**, 10–34.
- WILEY, R. H. & RICHARDS, D. G. (1982). Adaptations for acoustic communication in birds: sound propagation and signal detection, pp. 131–181 in: KROODSMA, D. E. & MILLER, E. H. (eds) *Acoustic Communication in Birds*. Vol. 1. New York, Academic Press.
- WILEY, R. H. (2005). Individuality in songs of Acadian flycatchers and recognition of neighbours. *Animal behavior*, **70**, 237–247.
- WILLIAMS, H., LEVIN, I. I., NORRIS, D. R., NEWMAN, A. E. M. & WHEELWRIGHT, N. T. (2013). Three decades of cultural evolution in Savannah sparrow songs. *Animal Behaviour*, **85**, 213–223.
- WILLIAMS, H., ROBINS, W. C., NORRIS, D. R., NEWMAN, A. E. M., FREEMAN-GALLANT, C. R., WHEELWRIGHT, N. T. & MENNILL, D. J. (2019). The buzz segment of Savannah sparrow song is a population marker. *Journal of Ornithology*, 10.1007/s10336-018-1611-7.
- YDENBERG, R. C., GIRALDEAU, L. A. & FALLS, J. B. (1988). Neighbours, strangers, and the asymmetric war of attrition. *Animal Behaviour*, **36**, 343–347.
- YEE, S. A., PUAN, C. L., CHANG, P. K. & AZHAR, B. (2016). Vocal individuality of Sunda scops-owl (*Otus lempiji*) in Peninsular Malaysia. *Journal of Raptor Research*, **50**, 379–390.
- ZAR, J. H. (1999). *Biostatistical analysis*. Upper Saddle River (NJ), Prentice Hall.

Table S1. Summary of means (\pm SD) and coefficients of variation (CV) of Savannah sparrow songs for 22 variables. Ten songs for each breeding period in 11 male Savannah sparrows in 2001 were analyzed. Frequency variables are reported in kHz and temporal variables in msec, except for duration of song (TS; sec); CV is reported as a percentage.

Variable	Breeding period				Totals
	Pre-pairing	Pairing & Egg-laying	Incubation	Nestling & Post-fledging	
Frequency attributes					
F1	8.7 \pm 0.3 (3.9)	8.4 \pm 0.4 (4.7)	8.7 \pm 0.5 (5.6)	8.4 \pm 0.3 (3.0)	8.4 \pm 0.4 (4.8)
F2	7.0 \pm 0.2 (3.0)	7.0 \pm 0.2 (3.1)	7.0 \pm 0.4 (6.2)	7.0 \pm 0.3 (4.2)	7.0 \pm 0.3 (4.4)
F3	6.3 \pm 0.8 (12.1)	6.3 \pm 0.8 (12.0)	6.3 \pm 0.9 (14.5)	6.3 \pm 0.7 (11.5)	6.2 \pm 0.8 (12.5)
F4	3.1 \pm 0.6 (20.6)	2.9 \pm 0.7 (22.8)	2.9 \pm 0.8 (25.8)	3.0 \pm 0.6 (19.5)	3.0 \pm 0.7 (22.4)
F5	7.0 \pm 0.4 (5.7)	7.1 \pm 0.4 (6.1)	7.0 \pm 0.5 (6.8)	7.1 \pm 0.4 (6.0)	7.0 \pm 0.4 (6.2)
F6	4.5 \pm 0.4 (8.7)	4.5 \pm 0.4 (9.1)	4.5 \pm 0.5 (10.7)	4.5 \pm 0.4 (8.7)	4.5 \pm 0.4 (9.3)
F7	1.8 \pm 0.5 (24.6)	1.8 \pm 0.4 (19.4)	1.8 \pm 0.5 (27.5)	1.8 \pm 0.4 (20.2)	1.8 \pm 0.4 (23.1)
F8	6.6 \pm 0.5 (7.6)	6.1 \pm 0.6 (9.8)	6.6 \pm 0.7 (11)	6.1 \pm 0.6 (9.4)	6.1 \pm 0.6 (10.1)
F9	1.8 \pm 0.7 (39.0)	1.9 \pm 0.7 (35.3)	1.7 \pm 0.8 (45.5)	1.8 \pm 0.7 (40.0)	1.8 \pm 0.7 (40.0)
Temporal attributes					
T1	2.9 \pm 0.3 (10.8)	2.6 \pm 0.3 (11.0)	2.8 \pm 0.3 (11.9)	2.6 \pm 0.3 (11.3)	2.6 \pm 0.3 (11.6)
T2	263.3 \pm 41.0 (15.6)	282.5 \pm 44.6 (15.8)	263.3 \pm 46.8 (17.2)	282.5 \pm 56.0 (20.0)	272.7 \pm 47.8 (17.4)
T3	77.1 \pm 9.8 (12.7)	73.3 \pm 9.0 (12.3)	77.1 \pm 10.0 (13.6)	73.3 \pm 9.5 (13.2)	73.3 \pm 9.8 (13.2)
T4	662.9 \pm 88.6 (13.4)	631.1 \pm 100.8 (16.0)	662.9 \pm 97.1 (15.2)	631.1 \pm 92.9 (14.9)	640.5 \pm 95.8 (15.0)
T5	50.6 \pm 9.7 (19.1)	50.9 \pm 9.9 (19.5)	50.6 \pm 10.0 (19.9)	50.9 \pm 10.7 (21.7)	50.3 \pm 10.1 (20.0)
T6	492.7 \pm 58.8 (11.9)	485.1 \pm 75.8 (15.6)	492.7 \pm 104.1 (23.0)	485.1 \pm 75.8 (16.3)	452.3 \pm 81.6 (17.2)
T7	36.2 \pm 5.5 (15.3)	38.9 \pm 6.8 (17.4)	36.2 \pm 7.5 (19.5)	38.9 \pm 5.7 (13.9)	38.4 \pm 6.6 (17.1)
T8	13.3 \pm 1.6 (12.3)	13.0 \pm 1.4 (10.4)	12.3 \pm 1.7 (13.7)	12.7 \pm 1.5 (11.6)	12.8 \pm 1.6 (12.3)
T9	2.8 \pm 1.4 (50.1)	3.0 \pm 1.0 (34.5)	3.6 \pm 1.6 (44.2)	3.2 \pm 1.3 (41.6)	3.2 \pm 1.4 (43.8)
T10	16.1 \pm 1.5 (9.6)	16.1 \pm 1.4 (8.9)	15.9 \pm 1.3 (8.0)	15.9 \pm 1.6 (10.0)	16.0 \pm 1.5 (9.1)
T11	8.9 \pm 1.5 (17.2)	8.0 \pm 1.1 (14.0)	8.4 \pm 1.5 (17.6)	8.5 \pm 1.3 (15.6)	8.4 \pm 1.4 (16.7)
T12	8.7 \pm 3.9 (44.2)	8.9 \pm 2.7 (30.3)	8.5 \pm 2.6 (30.2)	8.2 \pm 2.7 (32.6)	8.6 \pm 3.0 (34.9)
T13	17.6 \pm 3.6 (20.5)	16.8 \pm 3.0 (17.6)	16.9 \pm 3.0 (18.0)	16.7 \pm 2.8 (17.0)	17.0 \pm 3.1 (18.4)