Song structure and syllable and song repertoires of the Saffron Finch (Sicalis flaveola pelzelni) breeding in Argentinean pampas

María Juliana Benítez Saldívar & Viviana Massoni

View supplementary material

Published online: 25 Jun 2017.

Submit your article to this journal

View related articles

View Crossmark data

Taylor & Francis
Taylor & Francis Group

Check for updates

Song structure and syllable and song repertoires of the Saffron Finch (*Sicalis flaveola pelzelni*) breeding in Argentinean pampas

María Juliana Benítez Saldívar[a] [ID] and Viviana Massoni[a,b]

[a]CONICET-Universidad de Buenos Aires, Instituto de Ecología, Genética y Evolución (IEGEBA), Buenos Aires, Argentina; [b]Facultad de Ciencias Exactas y Naturales, Departamento de Ecología, Genética y Evolución, Universidad de Buenos Aires, Buenos Aires, Argentina

ABSTRACT

Empirical descriptions of vocal behaviour in avian communication are important in understanding its meaning and role in shaping the social and genetic relationships among individuals in a population. In this study, we provide the first detailed analysis of the vocal behaviour of the Saffron Finch (*Sicalis flaveola pelzelni*), a neotropical songbird found in rural and semi-open areas of Argentina that is frequently captured for the pet trade. We identify syllables, quantify the fine structural characteristics of the song, and describe the size and structure of the song repertoire. Further, we use networks to explore whether this species uses syntactical rules for creating their songs. Our analyses reveal that Saffron Finch males have a large syllable repertoire. Song repertoire size is not fixed, and birds recombine their syllables to produce highly variable songs. In addition, they sing with immediate variety, seldom repeating a song before switching to a new song and song sharing was very limited among our sampled individuals.

Introduction

Bird song is one of the most studied signals of animal communication and can show high complexity and variation in its production and delivery patterns (Marler and Slabbekoorn 2004). Songs are usually long (but see Krebs et al. 1978) and relatively complex vocalizations (Kroodsma and Parker 1977; Todt and Hultsch 1996), mostly produced by males along the breeding season in temperate zone (Catchpole and Slater 2008; Motes-Rodrigo et al. 2017; but see Illes and Yunes-Jimenez 2009; Odom et al. 2014; Cain et al. 2015 for examples of female songs), that are emitted spontaneously to signal identity, territorial ownership and sexual intentions (Catchpole and Slater 2008). They can be analysed at the note, syllable, or song level in terms of song composition and patterns of song delivery (Catchpole and Slater 2008).

Detailed descriptions of song structure are critical to understand the ontogeny, evolution, and function of bird song either as a signal of territorial defence or to mediate mate choice (Marler and Slabbekoorn 2004; Podos et al. 2004; Catchpole and Slater 2008). Pioneering song structure studies were conducted in northern temperate species, such as Chaffinches (*Fringilla coelebs*) (Slater 1983), American redstarts (*Setophaga ruticilla*) (Lemon et al. 1985), Swamp sparrows (*Melospiza georgiana*) (Clark et al. 1987) and Song Sparrows (*Melospiza melodia*) (Marler and Peters 1988). More recently, the song structure of tropical bird species has been analysed (Mennill and Vehrencamp 2005; Barker 2008; Vargas-Castro et al. 2012), leaving southern temperate birds relatively underrepresented (but see Baker et al. 2006; Greig and Pruett-Jones 2008; León et al. 2015). Although several studies have been conducted in Southern South America, some were focused on the relationship of song structure with the environment (Tubaro 1991; Kopuchian et al. 2004), while others examined song structure in relation to migration patterns (Areta 2012) or body size (García et al. 2014) and did not provide a comprehensive structural description of songs and the patterns of song delivery (but see León et al. 2015; dos Santos et al. 2016). Vocal descriptions, however, provide a valuable instrument for population census surveys and monitoring (McShea and Rappole 1997; Valderrama et al. 2008).

The Saffron Finch (*Sicalis flaveola pelzelni*) (P.L. Sclater 1872) is a small (ca.18 g), socially monogamous and multi-brooded secondary cavity nester that ranges from Southern Brazil and Eastern Bolivia to Central Argentina, South to La Pampa Province (Ridgely and Tudor 2009). They inhabit woods, rural and suburban areas (Narosky and Yzurieta 2010) and breed inside natural cavities in trees and Rufous Hornero (*Furnarius rufus*) nests, but also inside bridges and buildings holes and nest boxes (Mason 1985; Palmerio and Massoni 2009). They show delayed plumage maturation; second-year males are female-like and have a whitish belly with a brownish back, but after second-year males are overall golden yellow with an olive back-streaked with black (Narosky and Yzurieta 2010) and are the focus of this study. Their colour, granivorous habit, and lively pleasant and melodious song make the species a target for illegal capture as cage birds, which has likely caused local declines in Buenos Aires Province populations (Narosky and Di Giácomo 1993). Despite being the most wide-spread yellow-finch of South America (Ridgely and Tudor 1989), many aspects of their ecology and behaviour are unknown or poorly understood (but see Palmerio and Massoni 2009, 2011). Their song remains largely undescribed except for a single study that focused on the species' acoustic adaptations to urban environments (León et al. 2014); therefore, a thorough description of the song of the Saffron Finch is lacking to date.

We recorded the song of Saffron Finch males and conducted detailed acoustic analysis of their vocalizations (e.g. Hunter and Krebs 1979; Handford and Lougheed 1991). Our goals were to (1) provide a description of the fine structural characteristics of the syllables used, (2) assess the syllable and song repertoire sizes and (3) assess the components and organization of the song repertoires in a banded population of the species.

Methods

Study area

We studied Saffron Finches in a nest box assemblage placed in an agricultural field located in low-land pampas habitat surrounding the Instituto de Investigaciones Tecnológicas

de Chascomús (INTECH-CONICET) in Chascomús, Buenos Aires Province, Argentina (35°34′S, 58°01′W), from October to March of 2013–2014, 2014–2015 and 2015–2016. Nest boxes were mounted approximately 30 m from one another at a height of between 1.3 and 1.7 m on fence posts delimiting paddocks enclosing pastures or cattle; the paddocks are edged by a single line of tala (*Celtis tala*) or espinillo (*Acacia bonariensis*) native trees; the buildings are surrounded by mixed stands of tala, eucalyptus (*Eucalyptus* sp.), pine (*Pinus* sp.) and honey locust (*Gleditsia triacanthos*). The boxes measured $23 \times 15 \times 11$ cm of internal size and had an entrance hole 4 cm in diameter, a lateral door to monitor the nest's progress and a 'wigwag' trap to capture the breeding adults when they entered the box (further details in Palmerio and Massoni 2009). Birds were banded with a numbered aluminium ring and three plastic colour bands for identification at a distance.

Song recording and analysis

Spontaneously singing identified males were recorded at a distance of 20–30 m, while perched immediately adjacent to nest boxes or on a neighbouring tree during the hours of greatest activity, between 5:00–13:00 h and 16:00–19:00 h. We used a Marantz PMD 661 Professional Solid State Recorder a Sennheiser ME/K 66 shotgun microphone and set the recordings at a sampling rate of 44.1 kHz and 16-bit depth in the first two breeding seasons and of 48 kHz, 32-bit depth in the last one.

Syllables consist of a single note or a set of notes that are typically grouped together; we defined notes as continuous traces in a spectrogram. Songs were defined as a sequence of syllables arranged over a short-time interval separated from the following song for a silent interval of over 1 s (Garamszegi et al. 2005; Vargas-Castro et al. 2012; Sosa-López and Mennill 2014). We analysed 54 recordings from 14 males for a total of 1572 songs, with an average of 110 ± 11 (mean ± SE) songs per male (range = 46–173 songs), using Raven Pro 1.4 (Charif et al. 2010). Spectrograms were created using the Hann spectrogram window type with 256 samples, a discrete Fourier transform (DFT) size of 256 samples and a grid spacing of 2.9 ms. In this first survey, we focused on the description of syllables, songs and their organization.

Syllables, spectrographic measurements and song classification

We followed the classification of Catchpole and Slater (2008) and used syllables as the basic unit of songs (Hasselquist 1998; Marler and Slabbekoorn 2004; Eriksen et al. 2011; Vargas-Castro et al. 2012). To be considered as the same syllable, the assumed same syllables had to be similar in duration and overall shape (as in Palmero et al. 2012). In addition, the syllables had to be consistent in bandwidth, which allows classification with high certainty. The majority of the syllables are frequency-modulated tonal syllables, but trills are also present in Saffron Finches songs. We defined trills and trill-like syllables as a series of notes or syllables repeated three or more times (Sosa-López and Mennill 2014). All syllable identification was performed by the same researcher (M.J.B.S) and blindly assigned to each type with over 96% concordance by V.M.

We created a library of syllables in which letters were assigned to each distinct syllable type for further identification. Although human classification can be time consuming

and potentially subjective, previous studies indicate that it is reliable when compared with more advanced mathematical or computational methods (Botero et al. 2008; Deslandes et al. 2014). Syllable repertoire size was defined as the total number of unique syllable types recorded for each bird. We evaluated the cumulative number of new syllables detected as a function of the number of songs recorded, determined the relative positions of syllables within songs, and used the syllable catalogue to create a library of the sequences of syllables of each song.

We defined a song conservatively as a unique sequence of syllable types arranged in a certain order, ignoring variation if a particular syllable type was repeated once or twice in a given position within a song, so as to avoid overestimation of the number of different songs (as in Rendall and Kaluthota 2013). However, if a syllable type was repeated in a different position in the song i.e. after the occurrence of other intervening syllables it was counted as a distinct song (dos Santos et al. 2016). Therefore, identical songs must be composed of the exact same sequence of syllables. With the purpose of representing the variability in songs, we calculated the song versatility index (SVI) as the ratio between unique or different syllable types and the total number of syllables in each song (Gil and Slater 2000).

For each bird, we measured and averaged the following temporal and frequency variables of songs from the spectrograms: (a) song length measured from the beginning of the first syllable to the end of the last syllable in the song (s), (b) maximum frequency, as the highest frequency with energy in the song (kHz), (c) minimum frequency, as the lowest frequency in the song (kHz), (d) frequency bandwidth, as the difference between maximum and minimum frequencies in the song (kHz), (e) peak frequency, as the frequency of maximum power of the song (kHz), (f) mean number of syllables per song, (g) syllable rate i.e. syllables produced per unit time as in Geberzahn and Aubin (2014) and (h) total number of syllable types, as the total number of syllables performed by each individual.

Song repertoire and transitions between songs

Song repertoire size was defined as the number of different songs recorded from each bird, and song bouts were considered to be an undisturbed sequence of singing activity recorded within one recording session (Rutkowska-Guz and Osiejuk 2004). Song repertoire size was evaluated by inspecting the cumulative number of new songs as a function of the number of songs recorded. We analysed the use of songs by creating a song transition matrix for each individual (Deslandes et al. 2014; Weiss et al. 2014) with the Markov chain package (Spedicato 2016); by ordering precedent songs in columns and subsequent songs in rows, the matrices allow the quantification of first-order transitions between adjacent songs in the sequence of songs. Subsequently, we used the transition matrices to build networks of songs for similar-sized song bouts using the iGraph package in R (Csárdi and Nepusz 2006). In these networks, each song is represented by a node, and edges symbolize transitions between songs; these directed networks illustrate the order among nodes. All data analysis was performed in R 3.3.1 (R Core Team 2016); we report results as the mean ± SE.

Results

Song structure

The songs were 2.1 ± 0.31 s long and had a frequency bandwidth of 5.97 ± 0.12 kHz. They contained 5.5 ± 0.27 different syllable types and 7.3 ± 0.67 syllables per song that were produced at an average rate of 3.94 ± 0.12 syllables/s (Table 1). We did not identify a pattern to divide songs into introduction and terminal sections as in León et al. (2014).

Syllables and syllable repertoire size

Syllables had a constant and easily recognizable shape and bandwidth, which allowed consistent identification within each male song and among different males. We identified a total of 85 different syllable types from all birds, although males had an average syllable repertoire size of 25 ± 1.9 syllables (range: 10–35 per individual). Based on their shape and temporal and frequency characteristics, we identified several syllable categories (Figure 1) such as: down-slurred whistles (e.g. AR), fast vibrato (e.g. W) and other complex forms (e.g. AD). The population syllable repertoire is shown in Supplemental Figures S1 (a) and S1 (b). Most of the birds reached an asymptote of syllable type repertoire at 100 songs, some at 150 songs, and 2 males continued to add new syllables, although the syllable repertoire size increased rather slowly (Figure 2). The song versatility index was 0.81 ± 0.02, with a range of 0.5–0.9 (see Table 1 for the characteristics of the songs of each individual).

Syllable sequences and pattern of use

The frequency of use of syllables in the song of Saffron finches was uneven; the 10 most-used syllables accounted for 55% of the total use of syllables; they had diverse shapes and were composed of several elements. In contrast, 53 other syllables were rarely used and then by only a few birds; each of the latter represented ≤ 1% of the use of syllables and accounted for 18% of the total syllable use when pooled together. Finally, 17 other syllables had an intermediate prevalence. Although syllables do not have fixed positions within a song,

Table 1. Summary statistics (counts or means ± SD) for the sample of analysed songs of 14 male Saffron Finches.

| Bird ID	Song length (s)	Band-width (Hz)	Peak frequency (Hz)	Syllables song^{-1}	Syllable rate (syllables sec^{-1})	SVI	Syllable types song^{-1}	Syllable types
2753	2.3 ± 1.5	6.0 ± 0.9	6.0 ± 0.8	6.6 ± 3.6	3.5 ± 1.71	0.82 ± 0.18	4.9 ± 2.3	30
2479	2.3 ± 1.4	6.9 ± 1.3	5.9 ± 1.0	8.0 ± 5.0	3.7 ± 1.1	0.80 ± 0.17	6.0 ± 3.3	33
2824	1.6 ± 0.8	5.8 ± 0.7	6.4 ± 0.7	6.5 ± 2.6	4.3 ± 1.1	0.77 ± 0.11	5.0 ± 2.3	27
2892	2.0 ± 1.6	6.0 ± 1.0	6.5 ± 0.8	6.5 ± 4.9	3.9 ± 1.8	0.83 ± 0.15	5.2 ± 3.1	35
2841	1.5 ± 0.7	6.1 ± 0.8	6.4 ± 0.8	5.8 ± 2.7	4.1 ± 0.9	0.80 ± 0.17	4.4 ± 2.0	33
2792	2.0 ± 1.4	5.6 ± 0.9	6.1 ± 1.2	7.3 ± 3.6	4.0 ± 0.9	0.88 ± 0.12	6.2 ± 2.3	26
2411	6.0 ± 2.3	6.3 ± 0.8	5.7 ± 0.8	14.9 ± 13.2	3.1 ± 1.3	0.67 ± 0.24	7.3 ± 2.9	17
2973	1.6 ± 1.1	5.4 ± 1.0	6.3 ± 0.8	6.5 ± 3.5	4.2 ± 0.6	0.89 ± 0.14	5.5 ± 1.9	22
183	1.5 ± 0.4	5.2 ± 0.5	6.6 ± 0.7	5.2 ± 1.2	3.7 ± 0.9	0.88 ± 0.14	4.6 ± 1.3	10
2581	1.1 ± 0.4	6.0 ± 0.8	6.6 ± 0.6	4.5 ± 1.4	4.9 ± 3.7	0.88 ± 0.13	3.9 ± 1.3	18
184	1.3 ± 0.6	5.5 ± 0.9	6.3 ± 1.0	5.7 ± 2.3	4.6 ± 1.6	0.84 ± 0.15	4.7 ± 2.0	23
2890	2.5 ± 1.5	6.0 ± 0.6	6.2 ± 0.9	8.9 ± 4.6	4.1 ± 1.3	0.69 ± 0.19	5.6 ± 2.2	27
235	2.4 ± 1.1	6.6 ± 0.9	6.6 ± 0.8	8.1 ± 3.6	3.5 ± 1.2	0.75 ± 0.13	6.0 ± 2.7	23
69	2.1 ± 0.7	6.1 ± 0.7	6.2 ± 1.2	7.9 ± 2.1	3.8 ± 0.4	0.96 ± 0.07	7.5 ± 1.7	29
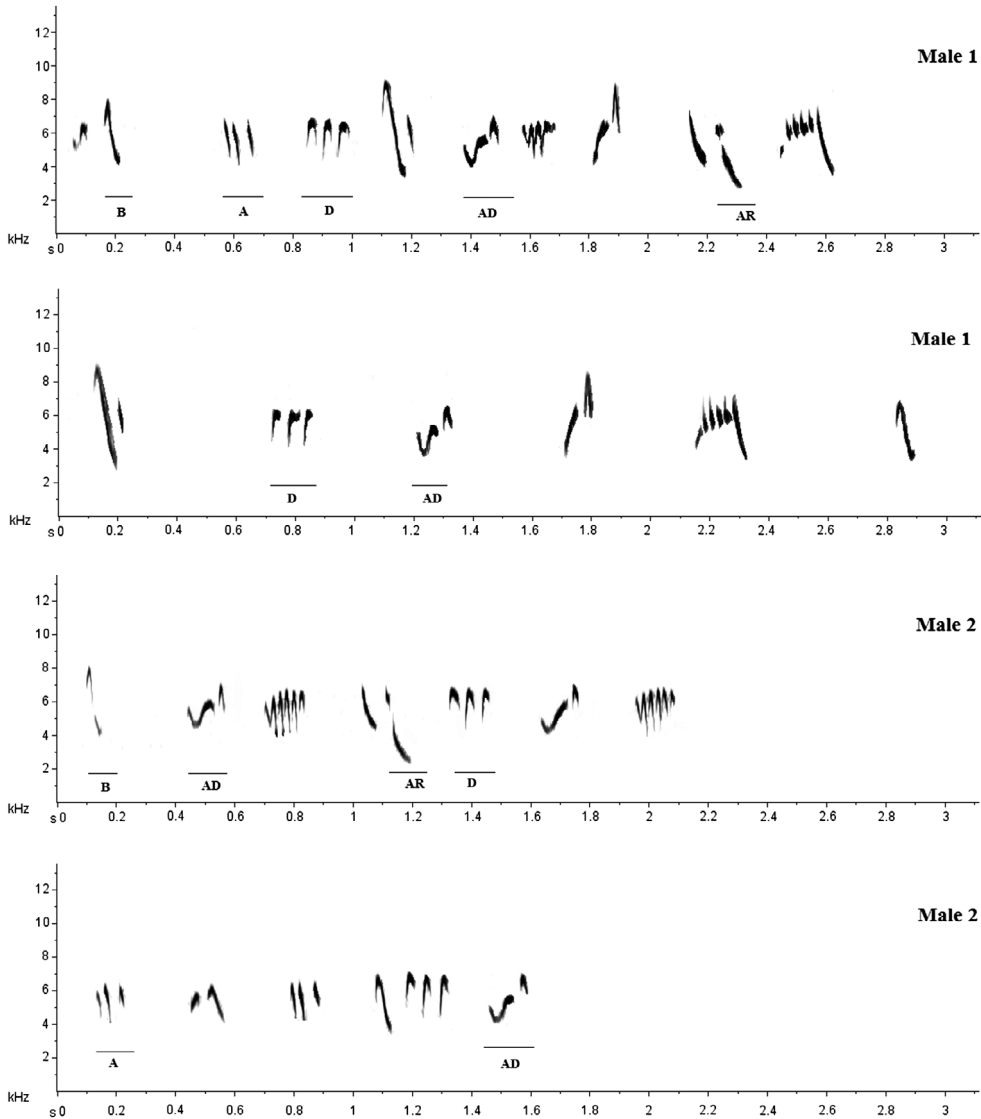
Figure 1. Two different songs from each of two different males. Syllable types common to songs used by both males are annotated to illustrate similarity in the forms of specific syllable types across males.

syllable placement showed a certain level of constraint and tended to appear more often in certain parts of the song than others (e.g. Figure 3, syllables B and E).

Song repertoires

Despite our conservative definition of song, there was tremendous diversity in the songs recorded. The cumulative number of new songs recorded showed continuous increases that never reached a plateau regardless of the size of the sample we analysed, as new songs were introduced continuously (Figure 4). By pooling together the 1572 songs recorded from all
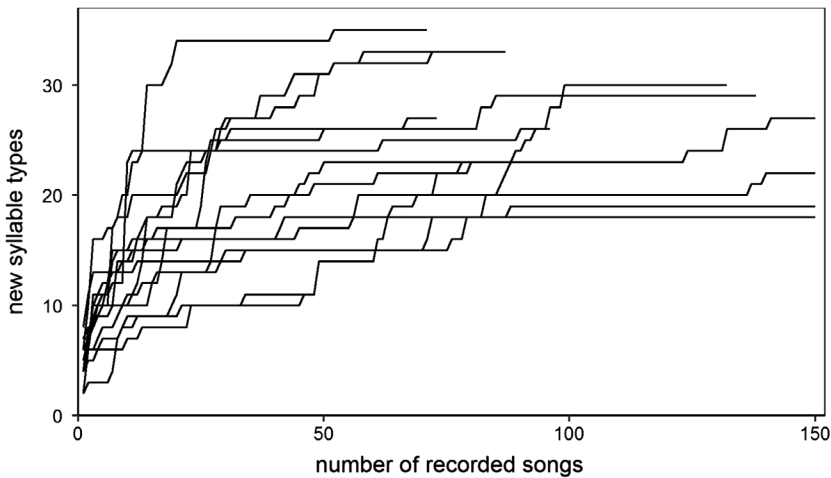
Figure 2. Syllable repertoire size and accumulation curves for each individual (*n* = 14); lines represent different males and show the time course over which males introduced new syllable types into their songs.
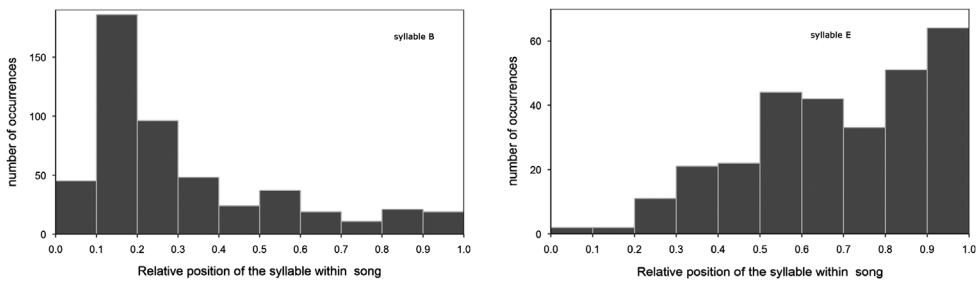

Figure 3. Relative position of two syllable types (B and E) in the songs of Saffron Finches.

males, we found 1289 different songs; only 22 songs in the pool matched in terms of the entire sequence of syllable types and were shared by just 2 or 3 males. Finally, the transitions between songs found in the networks showed that each male sang many different songs in succession and that repetitions of previously sang songs were infrequent (e.g. Figure 5(a) and (b)).

Discussion

We provide the first comprehensive description and analysis of syllable structure and repertoire, their combination into songs, and song usage in Neotropical Saffron Finch males breeding in Argentinean pampas, an essential first step in the study of the role of song in shaping the social and genetic relationships among individuals in the species.

Saffron Finch songs are short; their large average bandwidth indicates that the species has a wide-frequency range of singing, which concurs with results obtained by Tubaro and Lijtmaer (2006) for the genera *Pheucticus* and *Saltator*, particularly for species inhabiting open areas. The duration of song elements is also similar between the Saffron Finch and the
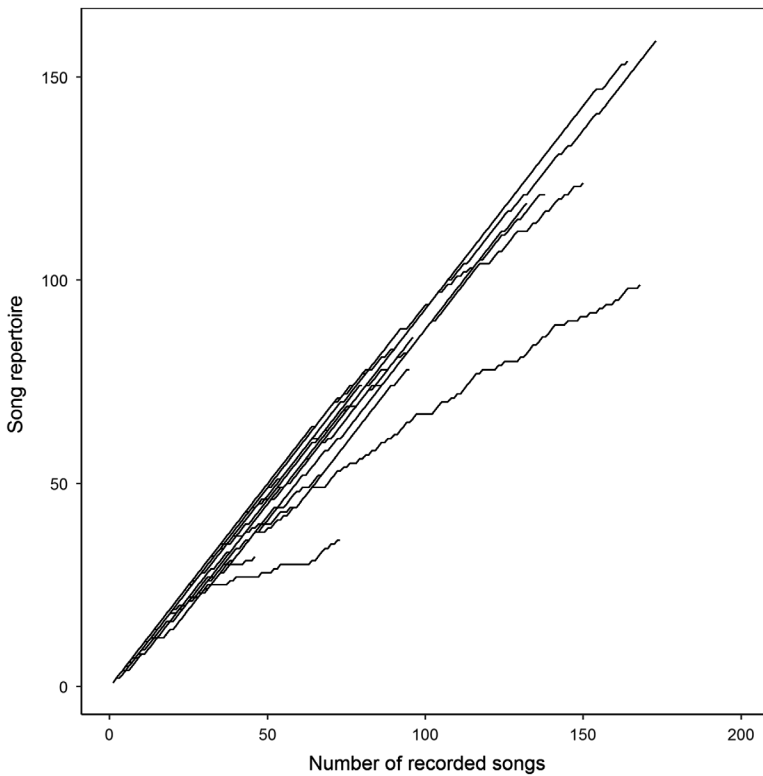
Figure 4. Song repertoire size and cumulative plot for each individual (*n* = 14); lines represent different males and show the time course over which males introduced new songs in the recordings.

Black-throated Saltator (*Saltator atricollis*), the Golden-billed Saltator (*Saltator aurantii-rostris*) and the Orinoco Saltator (*Saltator orenocensis*), which they studied. The described habitat for Saffron Finches includes woods and pasturelands in rural and suburban areas (Narosky and Yzurieta 2010). Our study site matches that description, and even though we offered nest boxes within forest patches, Saffron Finches never used them (V.M., pers. obs.). In our study area, they clearly preferred nest boxes located in mixed pampas grasslands with sparse trees from which they sing.

The mean syllable repertoire size of this population (10–35 syllables) was large, comparable to that of Southern House Wrens (*Troglodytes aedon chilensis*) (dos Santos et al. 2016), larger than that of Clay-coloured Thrushes (*Turdus grayi*) (Vargas-Castro et al. 2012) and much larger than that of the Golden-billed Saltator (*Saltator aurantiirostris*) (León et al. 2015). Our analysis shows that individual Saffron Finches deliver some syllables with more frequency than other birds, as occurs in other species with elaborate songs like spectacled warbler (*Sylvia conspicillata*) (Palmero et al. 2012) and brown-throated wren (*Troglogytes brunneicollis*) (Sosa-López and Mennill 2014). Some frequently used syllables were found preferentially at certain positions within songs, i.e. showing a lack of evenness in their use, as is the case in several wrens (Rendall and Kaluthota 2013; Sosa-López and Mennill 2014; dos Santos et al. 2016). The syllable repertoires of most Saffron Finch males reached an asymptote, suggesting that we conducted a suitable sampling effort; in the few cases where
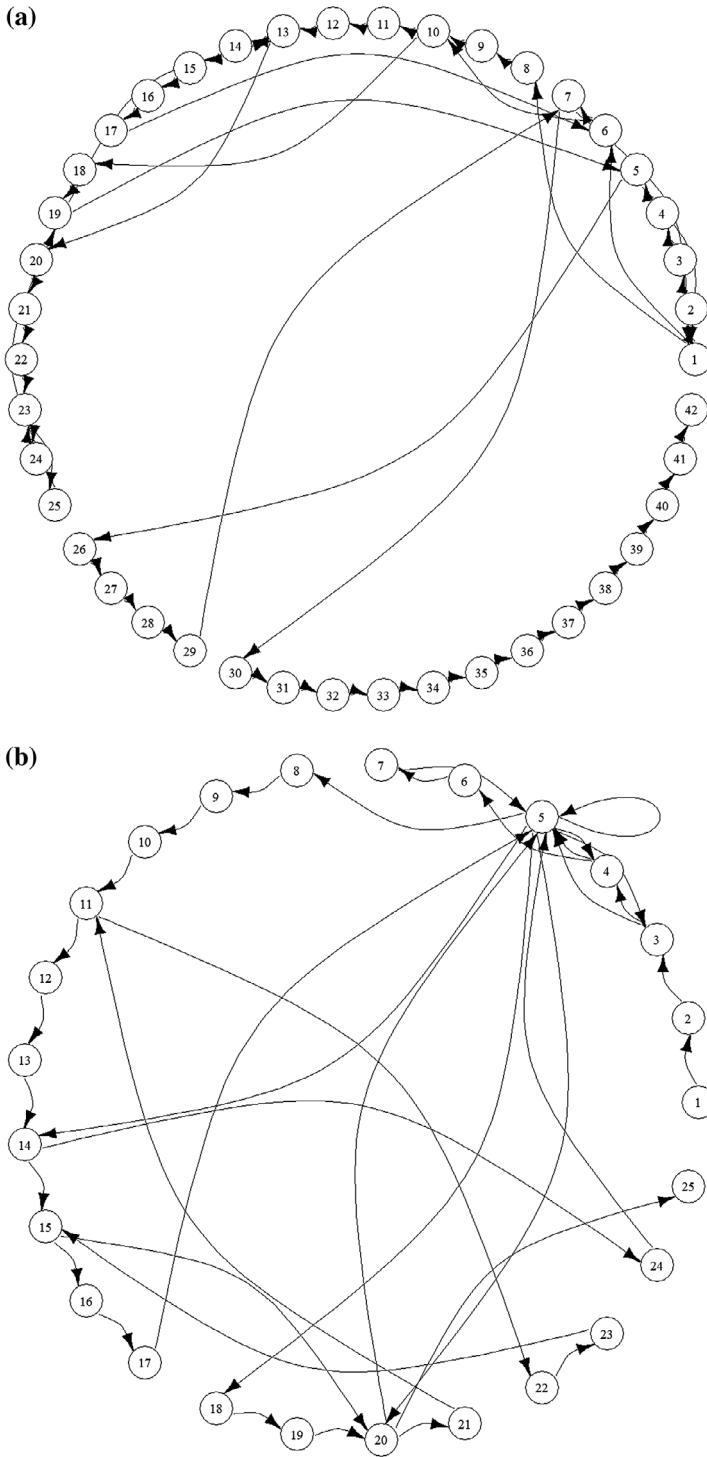
Figure 5. Transitions between songs in two selected Saffron Finch males: (a) individual singing in a quasi-linear pattern of song output, (b) individual singing a song multiple times within a singing bout.

asymptotes were not reached, the number of new syllables was levelling off, and a further increase in the syllable repertoire would occur at a slower rate if new syllables sporadically arose.

Saffron Finch males had a large average syllable repertoire of 25 syllables, with a low number of distinctive or unique syllables per individual. Songs were composed of a stable number of syllables that were, however, seldom repeated within a song. Males combined those syllables to produce a tremendous diversity in songs; the asymptotic curves illustrating new songs as a function of the number of songs recorded continued to increase and showed no apparent limit in the sample size obtained (Figure 4). Field experiments have demonstrated the importance of a large repertoire size for signalling during male-male competition (e.g. Krebs et al. 1978) and female choice (e.g. Searcy and Yasukawa 1996). Song repertoire size is, however, one of the simplest indexes of song complexity and may not be particularly diagnostic for species with highly complex songs (Botero et al. 2008; Cody et al. 2015); therefore, large repertoires have recently been described in detail in an attempt to understand the rules that govern the use of syllables and song sequences in the complex songs of certain species (Palmero et al. 2012; Weiss et al. 2014; Hedley 2015).

The variability in Saffron Finch songs was reflected in their song versatility index (0.81), which was higher than that reported for Southern and Northern House Wrens (0.46 and 0.39, respectively) despite having comparable individual syllable repertoires: 10–35 syllables in the Saffron Finch vs. 19–28 syllables and 19–24 syllables in the Southern and Northern House Wren, respectively. The difference is likely due to wrens repeating certain syllables, particularly at the end of their song. The high variability in song composition in this finch is due to the addition, subtraction or rearrangement of several syllables already present in previously sang songs. Had we considered the occurrence of successive repetitions of syllables within songs as new songs, the total number of shared songs among males would have been even lower.

The song networks illustrated certain patterns of song sequencing in the Saffron Finch; males delivered songs with immediate variety (Figure 5(a)), i.e. rarely repeating a song consecutively. By far, the most common transition between successive songs was to a different song, as in Sedge Warblers (*Acrocephalus arundinaceus*) (Catchpole 1976) and Hermit Thrushes (*Catharus guttatus*) (Rivers and Kroodsma 2000). They can, nonetheless, repeat a song just once when a quasi-linear pattern of song usage occurs (Figure 5(a)) or repeat a song multiple times within a singing bout (Figure 5(b)). In comparison, House Wrens are much more repetitive and only occasionally switched to a different song (dos Santos et al. 2016), frequently one with slight differences from the previously sang song (Rendall and Kaluthota 2013).

The extent of song sharing provides information about social interactions and the song learning process in a songbird species (Baker et al. 1986; Searcy and Andersson 1986; Beecher and Burt 2004), and songbirds differ in the number of songs shared between the individuals of a given population (Johnson 2006; Nicholson et al. 2007); Saffron Finch males shared only 1.4% of the songs sang at our study site. It is important to note, however, that some males recorded and analysed in this study were breeding in different years.

In their study of Saffron Finch song adaptation to urban noise, León et al. (2014) described songs as having an introduction and a trilled section, but we were unable to find such structure. Even though we detected some trills, their frequency of use and position within songs did not allow differentiating songs into subunits. The difference between the two studies

probably resides in that we specifically aimed to describe the vocalizations and analysed a large number of songs per individual in detail. Geographic variation in song can be an important marker of different subspecies and may play a role in speciation (Slabbekoorn and Smith 2002; Podos and Warren 2007), but the two studies were conducted in similar habitats located less than 500 km apart and not separated by relevant physical barriers, reducing the likelihood of song differentiation among populations. In spite of their relative abundance, breeding range, and extensive use as a cage bird, we know nothing about how the vocal behaviour of Saffron Finches varies within and among the five subspecies currently accepted in the literature (Gill and Donsker 2017). Meticulous syllable identification and analysis of song usage coupled with relatively large recording sessions will be necessary to determine whether there is population or geographic variation in the song of Saffron Finches.

Acknowledgements

Disclosure statement

No potential conflict of interest was reported by authors.

Funding

ORCID

María Juliana Benítez Saldívar http://orcid.org/0000-0002-1706-3185

References

Areta JI. 2012. Winter songs reveal geographic origin of three migratory seedeaters (Sporophila spp.) in Southern Neotropical grasslands. Wilson J Ornithol. 124:688–697.

Baker MC, Bjerke TK, Lampe H, Espmark Y. 1986. Sexual response of female great tits to variation in size of males' song repertoires. Am Nat. 128:491–498.

Baker MC, Baker MSA, Tilghman LM. 2006. Differing effects of isolation on evolution of bird songs: examples from an island-mainland comparison of three species. Biol J Linn Soc. 89:331–342.

Barker NK. 2008. Bird song structure and transmission in the Neotropics: trends, methods and future directions. Ornitol Neotrop. 19:175–199.

Beecher MD, Burt J. 2004. The role of social interaction in bird song learning. Curr Dir Psychol Sci. 13:224–228.

Botero CA, Mudge AE, Koltz AM, Hochachka WM, Vehrencamp SL. 2008. How reliable are the methods for estimating repertoire size? Ethology. 114:1227–1238.

Cain KE, Cockburn A, Langmore N. 2015. Female song rates in response to simulated intruder are positively related to reproductive success. Front Ecol Evol. 3:119.

Catchpole CK. 1976. Temporal and sequential organisation of song in the sedge warbler (*Acrocephalus Schoenobaenus*). Behaviour. 59:226–245.

Catchpole CK, Slater PJB. 2008. Bird song. New York, NY: Cambridge University Press.

Charif RA, Waack AM, Strickman LM. 2010. Raven Pro 14 user's manual. Ithaca, NY, Cornell Lab. of Ornithology.

Clark CW, Marler P, Beeman K. 1987. Quantitative analysis of animal vocal phonology: an application to Swamp Sparrow song. Ethol. 76:101–115.

Cody ML, Stabler E, Manuel H, Castellanos S, Taylor CE. 2015. Structure, syntax and "small-world" organization in the complex songs of California Thrashers (*Toxostoma redivivum*). Bioacoustics. 25:41–54.

Csárdi G, Nepusz T. 2006. The igraph software package for complex network research. InterJournal Complex Syst. 1695. http://igraph.org

Deslandes V, Faria LRR, Borges ME, Pie MR. 2014. The structure of an avian syllable syntax network. Behav Processes. 106:53–59.

dos Santos EB, Llambías PE, Rendall D. 2016. The structure and organization of song in Southern House Wrens (*Troglodytes aedon chilensis*). J Ornithol. 157:289–301.

Eriksen A, Slagsvold T, Lampe HM. 2011. Vocal plasticity – are Pied Flycatchers (*Ficedula hypoleuca*) open-ended learners? Ethology. 117:188–198.

Garamszegi LZ, Balsby TJS, Bell BD, Borowiec M, Byers BE, Draganoiu T, Eens M, Forstmeier W, Galeotti P, Gil D. 2005. Estimating the complexity of bird song by using capture-recapture approaches from community ecology. Behav Ecol Sociobiol. 57:305–317.

García NC, Barreira AS, Kopuchian C, Tubaro PL. 2014. Intraspecific and interspecific vocal variation in three Neotropical cardinalids (Passeriformes: Fringillidae) and its relationship with body mass. Emu. 114:129–136.

Geberzahn N, Aubin T. 2014. Assessing vocal performance in complex birdsong: a novel approach. BMC Biol. 12:217.

Gil D, Slater PJB. 2000. Multiple song repertoire characteristics in the willow warbler (*Phylloscopus trochilus*): correlations with female choice and offspring viability. Behav Ecol Sociobiol. 47:319–326.

Gill F, Donsker D. 2017. IOC World Bird List (v 71). http://www.worldbirdnames.org/

Greig E, Pruett-Jones S. 2008. Splendid songs: the vocal behaviour of Splendid Fairy-wrens (*Malurus splendens melanotus*). Emu. 108:103–114.

Handford P, Lougheed SC. 1991. Variation in Duration and Frequency Characters in the Song of the Rufous-Collared Sparrow, *Zonotrichia capensis*, with Respect to Habitat, Trill Dialects and Body Size. Condor. 93:644–658.

Hasselquist D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology. 79:2376–2390.

Hedley RW. 2015. Composition and sequential organization of song repertoires in Cassin's Vireo (*Vireo cassinii*). J Ornithol. 157:13–22.

Hunter ML, Krebs JR. 1979. Geographical variation in the song of the great tit (Parus major) in relation to ecological factors. J Animal Ecol. 48:759–785.

Illes AE, Yunes-Jimenez L. 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. Proc R Soc B. 276:981–986.

Johnson SL. 2006. Do American Robins acquire songs by both imitating and inventing? Wilson. J Ornithol. 118:341–352.

Kopuchian C, Alejandro Lijtmaer D, Luis Tubaro P, Handford P. 2004. Temporal stability and change in a microgeographical pattern of song variation in the rufous-collared sparrow. Anim Behav. 68:551–559.

Krebs J, Ashcroft R, Webber M. 1978. Song repertoires and territory defence in the great tit. Nature. 271:539–542.

Kroodsma DE, Parker LD. 1977. Vocal virtuosity in the brown thrasher. Auk. 94:783–785.

Lemon R, Cotter R, MacNally RC, Monette S. 1985. Song repertoires and song sharing by American redstarts. Condor. 87:457–470.

León EJ, Beltzer A, Quiroga M. 2014. El jilguero dorado (*Sicalis flaveola*) modifica la estructura de sus vocalizaciones para adaptarse a hábitats urbanos. Rev Mex Biodivers. 85:546–552.

León EJ, Beltzer AH, Olguin PF, César F, Urich GV, Alessio V, Cacciabué CG, Quiroga MA. 2015. Song structure of the golden-billed saltator (*Saltator aurantiirostris*) in the middle Parana river floodplain. Bioacoustics. 24:37–41.

Marler P, Peters S. 1988. The role of song phonology and syntax in vocal learning preferences in the Song Sparrow (*Melospiza melodia*). Ethol. 77:125–149.

Marler P, Slabbekoorn H. 2004. Nature's Music: the science of birdsong. San Diego, CA: Elsevier Academic Press.

Mason P. 1985. The nesting biology of some Passerines of Buenos Aires. Argentina Ornithol Monogr. 36:954–972.

McShea WJ, Rappole JH. 1997. Variable song rates in three species of passerines and implications for estimating bird populations. J F Ornithol. 68:367–375.

Mennill DJ, Vehrencamp SL. 2005. Sex differences in singing and duetting behavior of neotropical rufous-and-white wrens (*Thryothorus rufalbus*). Auk. 122:175–186.

Motes-Rodrigo A, Labra A, Lampe HM. 2017. Breeding experience and not age modulates the song development of pied flycatchers (*Ficedula hypoleuca*). Ethology. 123(3):197–204.

Narosky T, Di Giácomo AG. 1993. Las aves de la provincia de Buenos Aires: distribución y estatus. Buenos Aires, Argentina: Asociación Ornitológica del Plata, Vázquez Mazzini Ed., Literature of Latin America (L.O.L.A.).

Narosky T, Yzurieta D. 2010. Aves de Argentina y Uruguay: Guía de Identificación. In: 16th ed. Buenos Aires: Vasquez-Mazzini; p. 427.

Nicholson JS, Buchanan KL, Marshall RC, Catchpole CK. 2007. Song sharing and repertoire size in the sedge warbler (*Acrocephalus schoenobaenus*): changes within and between years. An Behav. 74:1585–1592.

Odom kJ, Hall ML, Riebel K, Omland KE, Langmore NE. 2014. Female song is widespread and ancestral in songbirds. Nat Commun. 5:3379.

Palmerio AG, Massoni V. 2011. Parental care does not vary with age-dependent plumage in male Saffron Finches *Sicalis flaveola*. Ibis. 153:421–424.

Palmerio AG, Massoni V. 2009. Reproductive biology of female Saffron finches does not differ by the plumage of the mate. Condor. 111:715–721.

Palmero AM, Illera JC, Laiolo P. 2012. Song characterization in the spectacled warbler (*Sylvia conspicillata*): a circum-Mediterranean species with a complex song structure. Bioacoustics. 21:175–191.

Podos J, Huber SK, Taft B. 2004. Bird song: the interface of evolution and mechanism. Annu Rev Ecol Evol Syst. 35:55–87.

Podos J, Warren PS. 2007. The evolution of geographic variation in birdsong. Adv Study Behav. 37:403–458.

R Core Team. 2016. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Rendall D, Kaluthota CD. 2013. Song organization and variability in Northern House Wrens (*Troglodytes aedon parkmanii*) in western Canada. Auk. 130:617–628.

Ridgely RS, Tudor G. 1989. The birds of South America, Vol 1: the oscine passerines. 4th ed. Austin: University of Texas Press.

Ridgely R, Tudor G. 2009. Field guide to the songbirds of South America The passerines. pp. 761. Austin: University of Texas Press.

Rivers JW, Kroodsma DE. 2000. Singing behavior of the hermit thrush. J F Ornithol. 71:467–471.

Rutkowska-Guz JM, Osiejuk TS. 2004. Song structure and variation in yellowhammers (*Emberiza citronella*) from western Poland. Polish J Ecol. 52:333–345.

Searcy WA, Andersson M. 1986. Sexual selection and the evolution of song. Annu Rev Ecol Syst. 17:507–533.

Searcy WA, Yasukawa K. 1996. Song and female choice: Ecology and evolution of acoustic communication in birds. New York: Cornell University Press, Chapter 25, Song and Female Choice, p. 454–473.

Slabbekoorn H, Smith TB. 2002. Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. Evolution. 56:1849–1858.

Slater PJB. 1983. Sequences of song in chaffinches. An Behav. 31:272–281.

Sosa-López JR, Mennill DJ. 2014. The vocal behavior of the Brown-throated Wren (Troglodytes brunneicollis): song structure, repertoires, sharing, syntax, and diel variation. J Ornithol. 155: 435–446.

Spedicato GA. 2016. Markovchain: discrete time Markov chains made easy.

Todt D, Hultsch H. 1996. Ecology and evolution of acoustic communication in birds Acquisition and performance of song repertoires: ways of coping with diversity and versatility. Ithaca, NY: Cornell University Press; p. 79–98.

Tubaro PL. 1991. Can *Troglodytes aedon* in Argentina "mimic" the songs of *Thryomanes bewickii*? Condor. 93:443–445.

Tubaro PL, Lijtmaer DA. 2006. Environmental correlates of song structure in Forest grosbeaks and saltators. Condor. 108:120–129.

Valderrama S, Parra J, Dávila N, Mennill DJ. 2008. Vocal behavior of the critically endangered Niceforo's Wren (*Thryothorus nicefori*). Auk. 125:395–401.

Vargas-Castro LE, S?nchez NV, Barrantes G. 2012. Repertoire size and syllable sharing in the song of the clay-colored thrush (*Turdus grayi*). Wilson J Ornithol. 124:446–453.

Weiss M, Hultsch H, Adam I, Scharff C, Kipper S. 2014. The use of network analysis to study complex animal communication systems : a study on nightingale song. Proc R Soc B. 281:20140460.