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Variación cultural en los cantos del cuatro ojos de jupa negra (*Melozone leucotis*) a través del tiempo

Tesis para optar por el grado de Licenciatura en Biología con énfasis en Zoología

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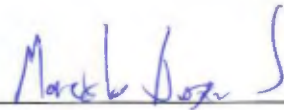
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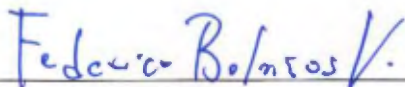
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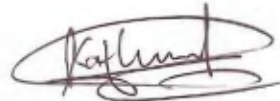
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ÍNDICE GENERAL

RESUMEN EN ESPAÑOL	7
PALABRAS CLAVE EN ESPAÑOL	8
RESUMEN EN INGLÉS	9
PALABRAS CLAVE EN INGLÉS	9
INTRODUCCIÓN	10
MÉTODOS	12
RESULTADOS	19
DISCUSIÓN	25
LITERATURA CITADA	30

ÍNDICE DE CUADROS

TABLE 1. Classification of song types in common and less common.....	18
TABLE 2. Regression of the curves of cumulative song types for the four populations using the number of new males per year (independent variable) and the total song types in the population repertoire (dependent variable).....	20
TABLE 3. Linear regressions testing the probability of permanence of the common and less- song types in four populations of White-eared Ground-Sparrows in Costa Rica through years.....	23

ÍNDICE DE FIGURAS

- FIGURE 1.** Map of the study areas, showing the four populations: (A) Universidad de Costa Rica main campus; (B) Instalaciones Deportivas of Universidad de Costa Rica; (C) Getsemaní, Heredia; and (D) Jardín Botánico Lankester, of White-eared Ground-Sparrows in Central Valley, Costa Rica. Maps based on Google Maps **14**
- FIGURE 2.** Sound spectrogram of a typical solo song with three sections of White-eared Ground-Sparrows showing the (1) initial section with elements of high frequency, (2) middle section with modulated frequency elements; and (3) final section with a short trill **16**
- FIGURE 3.** Curve of cumulative song types according to cumulative males in four populations of White-eared Ground-Sparrows in Costa Rica. Each point represents a sampled year. DEP: Instalaciones Deportivas of Universidad de Costa Rica; UCR: Universidad de Costa Rica main campus; HDIA: Getsemaní, Heredia; JBL: Jardín Botánico Lankester **20**
- FIGURE 4.** Clusters based on the Sørensen Index of similarity comparing (A) song types (N = 42 song types) in males' repertoire of White-eared Ground-Sparrows between years, and (B) males' identity (N = 96 males) in different years. The letters next to the branches represent each population sampled (UCR: Universidad de Costa Rica campus; DEP: Instalaciones Deportivas of the university; HDIA: north of Heredia; JBL: Jardín Botánico Lankester). When years are clustered at the end of the branches, it means they show similar patterns of repertoire use and male's replacement these years **22**
- FIGURE 5.** Probabilities of permanence for common and less-common song types in four populations of White-eared Ground-Sparrows in Costa Rica. Dotted lines represent timeline adjusted to linear regression. DEP: Instalaciones Deportivas of Universidad de Costa Rica; UCR: Universidad de Costa Rica main campus; HDIA: Getsemaní Heredia; JBL: Jardín Botánico Lankester..... **24**

ÍNDICE DE MATERIAL SUPLEMENTARIO

SUPPLEMENTARY MATERIAL TABLE S1. Probabilities of common types of songs in four populations of White-eared Ground-Sparrows in Costa Rica	38
SUPPLEMENTARY MATERIAL FIGURE S1. Example of recombination in solo song types of White-eared Ground-Sparrows as consequence of song learning by imitation. T53 was a recombination from common song types T2 and T3	41
SUPPLEMENTARY MATERIAL FIGURE S2. Example of improvisation in solo song types of White-eared Ground-Sparrows as consequence of song learning by imitation. An additional element was integrated in T49 from the original T16.....	42

RESUMEN EN ESPAÑOL

En aves cantoras, el proceso de aprendizaje de canto resulta de la transmisión cultural entre generaciones. Como consecuencia de este proceso y la evolución cultural de los cantos, se puede dar una variación microgeográfica entre poblaciones de la misma especie. Esto es, individuos vecinos comparten cantos similares, pero difieren a los cantos utilizados por otros conespecíficos que habitan a unos cuantos kilómetros de distancia. La variación de los cantos a una escala microgeográfica ha sido extensamente estudiada en aves de zonas templadas. Sin embargo, para las especies tropicales, el estudio de esta variación y su relación con la transmisión cultural del canto permanecen poco estudiados. Dada la presencia de variación microgeográfica en los cantos del cuatro ojos de jupa negra (*Melozone leucotis*: Passerellidae, Aves), una especie tropical, me enfoqué en entender la variación cultural y la permanencia de los cantos del macho en diferentes poblaciones a través del tiempo. Analicé el cambio de repertorio en los machos en un periodo de ocho años para determinar si la variación geográfica entre poblaciones es estable o cambia con el tiempo. Grabé los cantos de 96 machos anillados, de marzo a julio, 1 a 4 días por macho, para cuatro poblaciones en el Valle Central de Costa Rica, por ocho años (del 2011 al 2018). Utilizando el software Raven Pro, analicé 10 360 cantos, los cuales agrupé en 42 tipos según su estructura fina en el espectrograma, para comparar la composición de los repertorios por años y poblaciones. Para explicar la variación cultural, examiné si el recambio de machos influye en los cambios de composición de repertorio. Estimé la probabilidad de diferentes tipos de cantos de permanecer en la población basada en la frecuencia con que cada individuo (según su supervivencia) emitió cada tipo de canto. Encontré que la variación microgeográfica de los cantos es estable con el tiempo. Esto se

debió a una alta similitud dentro de los repertorios de las poblaciones dada la alta utilización de cantos comunes. Por otra parte, la variación encontrada dentro de cada población fue explicada por el recambio de los machos, la frecuencia de uso de cada tipo de cantos, y mutaciones culturales en la transmisión del canto a través de las generaciones (como la improvisación y la recombinación para producir nuevos y diferentes cantos en cada población). Sugiero que el cuatro ojos de jupa negra aprende sus cantos principalmente en sus territorios reproductivos a partir de sus vecinos reproductivos, dado el patrón de cantos, pero no descartó la posibilidad de que los aprendan de sus territorios natales, pues los machos tienden a dispersarse. Finalmente, con este estudio siento las bases para la investigación en la transmisión cultural y la variación asociada en los cantos de los machos de un pinzón neotropical.

Palabras clave: aprendizaje vocal, patrón de cantos, evolución cultural, Costa Rica

ABSTRACT

Microgeographic variation and dialects has been extensively studied in temperate species. However, for most tropical birds, these topics remain poorly studied. In this study, I focus on understanding the permanence and cultural evolution of the song in White-eared Ground-Sparrows. I analyzed repertoire changes in males of White-eared Ground-Sparrows over a period of eight years to determine if microgeographic variation is stable or change through time. I sound-recorded 96 banded males in four populations from 2011-2018 in Costa Rica, recording each male from one to three days, for 1 h/day each year. I analyzed 10 360 songs, grouped in 42 song types according to their fine structural features (duration, frequencies, and elements form), to compare the repertoire composition. To explain cultural variation, I examined how males' replacement affects repertoire changes within populations. In addition, I estimated the probability of different song types to remain within the population based on the frequency of individuals that emit each song type (corrected by the probability of males to survive), therefore determining if it affects microgeographic variation through time. Populations showed microgeographic variation with stability and persistence through time, and some variation explained by the males' replacement, cultural mutations (like improvisation and recombination), and the frequency of use of song types. I suggest that ground-sparrows learn their songs mainly in their breeding territories from their breeding neighbors, due to the song patterns, but I cannot discard that they also were learning their songs in their natal territories. In this study, I settled the basis on cultural transmission and variation in male solo songs of a Neotropical sparrow.

Keywords: vocal learning capacity, song patterns, cultural evolution, Costa Rica

INTRODUCTION

Many animal species (e.g., cetaceans, rodents, bats, frogs, insects, and birds) use acoustic signals for communication (Ladich and Winkler 2017). Vocalizations have different functions and are used in different social contexts (Seyfarth and Cheney 2010). Vocalizations, for instance, are used to maintain bonds with the mate and the offspring, to attract females and repel other males (Marler and Slabbekoorn 2004). Vocalizations in animals can be innate (do not need to copy a tutor or previous learning), as the case of nonhumans primates (e.g. gibbon and chimpanzees), or learned through imitation of their conspecific adults, like bats, whales, and songbirds (Colbert-White et al. 2014).

In songbirds, the song learning process results from cultural transmission among generations, from tutors to pupils (Baptista and Gaunt 1997; Catchpole and Slater 2008). Behavioural traditions, as songs in this case, transmitted culturally are known as “memes” (Lynch 1996, Dawkins 2016). Memes suffer mutations introduced principally by two mechanisms: point (changes in songs by copy-error or improvisation) and recombination (new creations from original song materials; (Lynch et al. 1989, Nelson et al. 2004). These changes and mutations conduct to cultural evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). Two fundamental processes that define the rate of cultural evolution are: (1) the way in which traditions (e.g, songs) are transmitted across generations, and (2) the demographic success of individuals with specific traditions (Gibbs 1990). In the first case, investigations focus on when, where, and from whom songbirds learn to sing, in association with dispersal and genetic patterns, and song sharing (McGregor and Krebs 1982, Lachlan and Slater 2003, Riebel et al. 2015, Graham et al. 2017). The second one is related, for example, to the survival of individuals or their

reproductive success (Ince et al. 1980, Gibbs 1990). Cultural evolution has been demonstrated in Common Chaffinch (*Fringillia coelebs*; Ince et al. 1980; Riebel et al. 2015), Indigo Bunting (*Passerina cyanea*; Thompson 1970), and Black-headed Bunting (*Emberiza melanocephala*; Barišić et al. 2018).

The microgeographic variation of songs is a consequence of song learning and cultural evolution (Catchpole and Slater 2008), and this refers to differences among neighboring populations whose close geographic proximity makes direct interbreeding and social interaction possible between them; often in a scale up to 10 km (Mundinger 1982, Baker and Cunningham 1985). There are some hypotheses to explain the microgeographic variation in songbirds. One of them, the genetic adaptation hypothesis, states that song matching may promote local recognition among individuals, thus leading to fine-tuned genetic adaptation to local environments (McGregor and Krebs 1982, Baker and Cunningham 1985, Loughheed and Handford 1992). Also, the deceptive mimicry hypothesis states that young males attempting to establish territories prefer to copy the songs of an established and successful adult (Payne 1981, 1982; Rohwer 1982, Baker and Cunningham 1985). A third one, the habitat matching hypothesis, states that specific songs may be adapted to particular acoustic conditions of the local neighborhood, especially in species that occur across a wide range of habitats with different environmental conditions (Hansen 1979, Gish and Morton 1981, Slater 1989).

Microgeographic variation between areas is more obvious in species where each bird sings only one or a few song types and has little variation within the area (Catchpole and Slater 2008) such as the European Redwing (*Turdus iliacus*; (Bjerke and Bjerke 1981, Espmark et al. 1989) and White-crowned Sparrow (*Zonotrichia leucophrys*; (Baptista

1975, 1977; Nelson et al. 2004). However, for most Neotropical bird species, the topics of microgeographic variation related to vocal learning and cultural transmission remain poorly studied (Koetz et al. 2007, Vargas-Castro et al. 2015), because most of these studies have been conducted in temperate species.

In this study, I focus on understanding the cultural evolution of songs in the White-eared Ground-Sparrows (*Melospiza leucotis*: Passerellidae), because it was found in two years-study, a microgeographic variation in this tropical species (Sandoval et al. 2014). Therefore, it is a good model to understand cultural transmission and song variation. I analyze the repertoire changes in color-banded males of White-eared Ground-Sparrows following them during eight years, to determine if microgeographic variation is stable or change through time. To explain cultural variation, I examined if the replacement of males inside the population affects the repertoire changes within that population. If new males bring new songs, I expect to find a positive correlation between the number of new males and the total repertoire for the population. In addition, I estimate the probability for specific song types to remain within the population according to their frequency of use (corrected by the survival probability of males that sing that song). I expect a positive correlation between the frequency of use in a specific song type and the probability for a particular song to remain within the population.

METHODS

Study site

I collected recordings of 96 White-eared Ground-Sparrows during eight consecutive breeding seasons (March to July 2011-2018) in four populations in the Central Valley, Costa Rica. (1) The main campus Universidad de Costa Rica, San José province (UCR;

09°56'15.001"N, 84°3'1.809" W; elevation 1200 m asl; 31.5 ha), with 19 males sampled. This area includes buildings, gardens, parking lots, a second growth riparian forest, and is surrounded by two of the principal roads in the area (Figure 1A). (2) Instalaciones Deportivas, Universidad de Costa Rica, San José province (DEP, 09°56'41.981" N, 84°2'43.258" W; elevation 1200 m asl; 25 ha) with 22 males sampled. This is an urban area that includes grasslands, secondary forest, and sports courts; this population is separated from UCR population by ca. 500 m (Figure 1B). (3) Getsemaní, San Rafael, Heredia Province (HDIA, 10°1'36.882" N, 84°6'58.15" W; elevation 1200 m asl; 20.1 ha) with 28 males sampled. It includes coffee plantations and secondary forest; there is an additional extensive area of second growth vegetation that extends far beyond the population limit (Figure 1C). (4) Jardín Botánico Lankester, Cartago Province (JBL, 09°50'22.501" N, 83°53'27.035" W; elevation 1400 m asl; 11 ha), with 24 males sampled. This is the population in the smallest area, which includes a secondary forest and gardens, surrounded by grassland and buildings; the closest forest patch is at approx. 500 m away (Figure 1D). I sound recorded all males present in each study area during the breeding season, except in HDIA population since it covers an extensive area and a riparian forest that serves as a corridor that connects multiple forest patches (Figure 1C), so I sampled those birds in patches close to the road. It is important to emphasize that I classified the populations according to song patterns, not necessarily there are populations of birds (Mundinger 1982).



FIGURE 1. Map of the study areas, showing the four populations: (A) Universidad de Costa Rica main campus; (B) Instalaciones Deportivas of Universidad de Costa Rica; (C) Getsemaní, Heredia; and (D) Jardín Botánico Lankester, of White-eared ground-sparrows in Central Valley, Costa Rica. Maps based on Google Maps.

Song pattern

White-eared Ground-Sparrows produce three types of vocalizations: calls (*chips* and *tseet*), male solo songs, and duets (produced by the male and female members of the pairs; (Sandoval and Mennill 2013, Sandoval et al. 2016). The solo song is only produced by males during the breeding season and is used for female attraction (pair formation and extra-pair copulations; Sandoval et al. 2016). This song is composed generally by three sections (Figure 2): (1) the initial section that have high frequency and short duration elements, very similar to *chip* call elements; (2) the middle section that have one or two

modulated frequency elements; and (3) the final section composed of a trill (Sandoval et al. 2016). Each male have a repertoire of two to eight song types that does not change between years, and males within a population have more similar songs between them than with males in other populations (Sandoval et al. 2014b, 2016).

Recording techniques

I recorded each male using the focal recording method, following one individual for 1h, from 0500–0600 h. Each male was recorded from one to four days per year, depending on how much each bird sang. All recordings were conducted during the breeding season, from March to June 2011–2019 (Sandoval and Mennill 2012, Sandoval et al. 2016). I recorded songs using a Marantz PMD 661 digital recorder (recording format: WAVE; sampling rate: 44.1 kHz; accuracy: 24 bits) and a Sennheiser K6/ME66 shotgun microphone. All males were color-banded with a unique color combination and a metallic numbered band. I recorded arriving and departing males in each population.

Vocal measurements

I visually classified the songs into different types based on their appearance on sound spectrograms, mostly in the shape of the elements in each song section (Sandoval et al. 2014b, 2016). All song types were compared to an acoustic library developed for White-eared Ground-Sparrows (Sandoval et al. 2014b), and extended with the new song types of this study. In some cases, within the same song type, the number of elements in the initial section varied subtly among individuals, because different males added or omitted some elements, and/or varied the length of the trill in the final section. However, the number of elements in the middle section did not vary among songs of the same type. Thus, I

classified as the same song type, all those songs that had similar fine structural features and contained the same number of elements in the middle section, but may vary in terms of the introductory or final elements (Figure 2). I classified the songs using the spectrogram window in Raven Pro 1.4 sound analysis software (Center for Conservation Bioacoustics 2011). I set the sound window used as follows: Hann type 50 % overlap, 256 kHz samples, with a frequency resolution of 188 Hz.

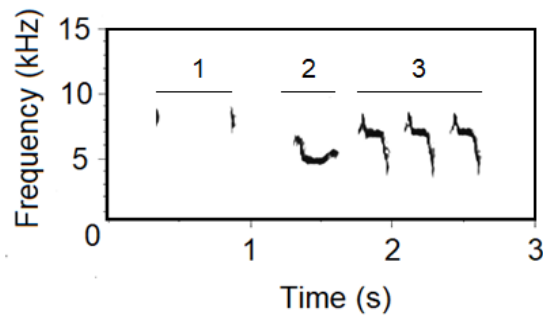


FIGURE 2. Sound spectrogram of a typical solo song with three sections of White-eared Ground-Sparrows showing the (1) initial section with elements of high frequency, (2) middle section with modulated frequency elements; and (3) final section with a short trill.

Statistical analysis

I constructed a song cumulative curve for each of the four populations using the number of new males per year (independent variable) and the total song types in the population repertoire (dependent variable) and the accumulation curves was fitted to a logarithmic regression to test. I conducted an Analysis of Covariance (ANCOVA) to compare the best fitted curves among populations. Hence, I used the populations as fixed factors (four levels), cumulative males as a covariable (quantitative), and repertoire size as the dependent variable (quantitative). I also used Tukey *post hoc* comparisons with an alpha of 0.05 to examine statistical differences between pairs of populations.

I estimated the similarity of song types across consecutive years in each population using the Sørensen index (a presence/absence index; Sørensen 1948). In addition, I estimated the similarity of banded males' composition according to consecutive years in each population using the Sørensen index. Then I compared both clusters to obtain possible patterns between years and evaluate the effect of males' and song types' occurrence. For both clusters, I only used data of the day with the largest number of songs recorded per male. This index values range from 0 to 1, where values close to 0 indicate low of similarity of song types or males between consecutive years and values close to 1 represent a high similarity (Sørensen 1948). I performed cluster analyses to depict the pattern of song types or males similarity between years using single linkage as cluster union based on the Sørensen index of similarity. I used PAST to conduct these analyses (Hammer et al. 2001).

I estimated the probability of song types to remain in the population using the two most common and two less-common songs in each population, using only the data of the day with the largest number of songs recorded per male. Common and less-common song types in each population were selected according to two criteria: the percentage of males in the population that sing the song and the percentage of their frequency of use in each male repertoire. The song types used in each population and specific percentages are summarized in Table 1. The probabilities of permanence of song types were estimated considering the frequency of use of each song type (number of times that all males used a specific song type, in sessions of one hour per breeding season) from 2011-2018. The frequency of use was corrected by the survival probability of the males, as reported by Juárez (2018) for the same populations and time period.

TABLE 1. Classification of song types in common and less common

Classification	Population	Song type	% Males	% Frequency of use
COMMON	UCR	14	90	28.8
		18	80	23.7
	DEP	13	72.7	17.8
		35	68.2	26.5
	HDIA	2	82.8	39.6
		3	100	32.6
	JBL	21	79.2	40.5
		42	100	38.1
LESS COMMON	UCR	16	80	15.2
		32	65	11.9
	DEP	37	54.5	8.0
		38	54.5	9.9
	HDIA	1	51.7	12.1
		29	13.8	3.8
	JBL	12	45.8	11.9
		44	29.2	7.8

The probability of permanence of a particular song type over consecutive years was calculated using the proportion of song frequency (frequency of use of the song type divided by all the recorded songs) multiplied by all males in the population corrected by the survival probability of those years. I used the following formula:

$$P_{T1,Y2} = [(F/W)_{Y1} * S_{Y1,2}]_{Mn}$$

Where $P_{T1,Y1}$ = probability of the specific song type (T1) in year 2 (Y2); $\left(\frac{F}{W}\right)_{Y1}$ = proportion of frequency (F) of a particular song, divided by total of songs of the population (W) in year 1. $S_{Y1,2}$ = probability of survival from year 1 to year 2. Mn = all males that sang that particular song from year 1 to year 2, based on the survival data for these populations (Juárez 2018). Likewise, I calculated this probability for the other years. I conducted simple linear regressions to determine if the probability of permanence of song

types increases, decreases, or remains unchanged through time within each population. Years were included as independent variable and the probabilities of song types as the response variable.

Finally, I compared the probabilities of permanence for the selected song types into consecutive years using a binomial test. I used total number of repetitions of each song type as the observed frequency, the probability of permanence of the previous year as expected frequency, and the proportion of songs (observed divided by total) as associated probability. Significant p-values indicate that the occurrence of a song type in the next year was lower or higher than expected by the test.

RESULTS

I measured 10 360 songs and identified a total of 41 types from all birds and locations. I found 14 song types in 2 264 songs at UCR population, 22 song types in 2 853 songs in DEP, 13 song types in 3 537 songs in HDIA, and 6 song types in 1 706 songs in JBL. The number of new song types increased throughout the eight years. Repertoire size was positively related with the number of new males that arrived to each population each year (Table 2, Figure 3). The number of new songs increased each year in DEP population (Figure 3), but new song types did not appear after the sixth year in the UCR population (Figure 3), the seventh year in HDIA (Figure 3), and I did not record new song types after the third year in JBL (Figure 3). The UCR and DEP populations showed similar accumulation curves of new song types through time, and differed from those of HDIA and JBL populations (Figure 3, ANCOVA: $F_{3, 524} = 56.05$, $P < 0.0001$).

TABLE 2. Regression of the curves of cumulative song types for the four populations using the number of new males per year (independent variable) and the total song types in the population repertoire (dependent variable).

Population	Logarithmic regression (R^2)	T test (t)	P-value
UCR	0.79	4.01	0.007
DEP	0.96	8.92	<0.001
HDIA	0.93	7.09	<0.001
JBL	0.71	2.61	0.040

P-values in bold mean probability statistically significant ($P < 0.05$)

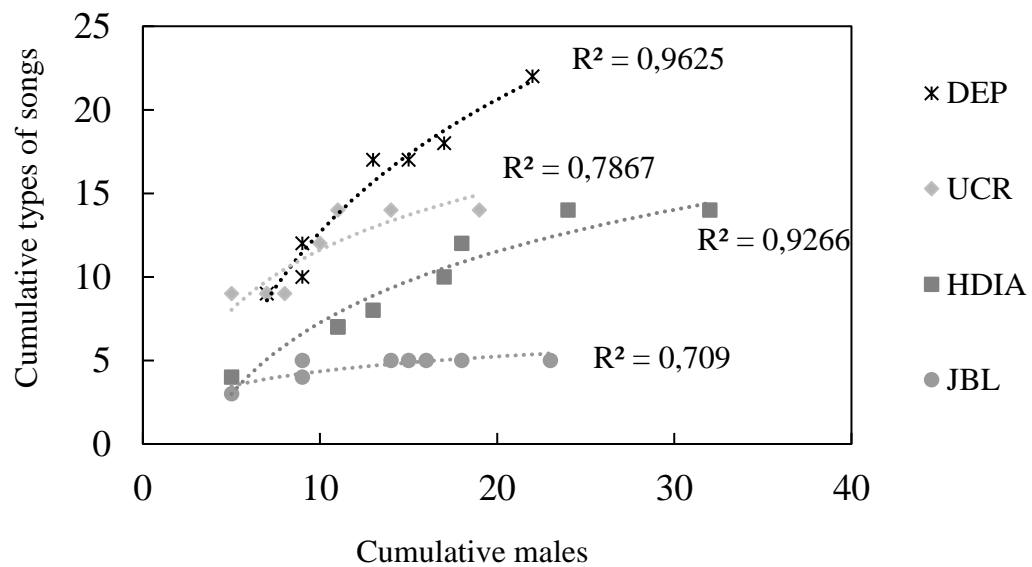


FIGURE 3 Curve of cumulative song types according to cumulative males in four populations of White-eared Ground-Sparrows in Costa Rica. Each point represents a sampled year. DEP: Instalaciones Deportivas of Universidad de Costa Rica; UCR: Universidad de Costa Rica main campus; HDIA: Getsemaní, Heredia; JBL: Jardín Botánico Lankester. Curves are adjusted to logarithmic regression.

Although new individuals introduced new songs, the Sørensen similarity index showed that the repertoires of solo songs remained similar during eight years within populations. The similarity in song types ranged from 60 to 100 % among years (Figure 4A). The cluster analysis showed that consecutive years were more similar among them (Figure 4A). JBL population showed the lowest similarity in 2013 relative to the other years, close to 50 %, this because during 2013 I only recorded four songs classified in two song types of one male, likely due to the effect of an extensive drought caused by El Niño event, which affected reproduction and consequently reduced singing activity (Figure 4A). The replacement of males (arriving and departing males) through consecutive years varied among populations. For the UCR population, the similarity of males ranged from 20 to 90 %, for the DEP population, from 30 to 100 %; for the HDIA population, from 20 to 100 %; and for the JBL population, from 20 to 90 % (Figure 4B). Comparing both cluster analyses, repertoire composition and males' replacement by years, I found matchings between clusters for three populations (DEP, UCR, and HDIA) and a tendency of consecutive years to cluster together in both clusters, except for JBL population (Figure 4A y B).

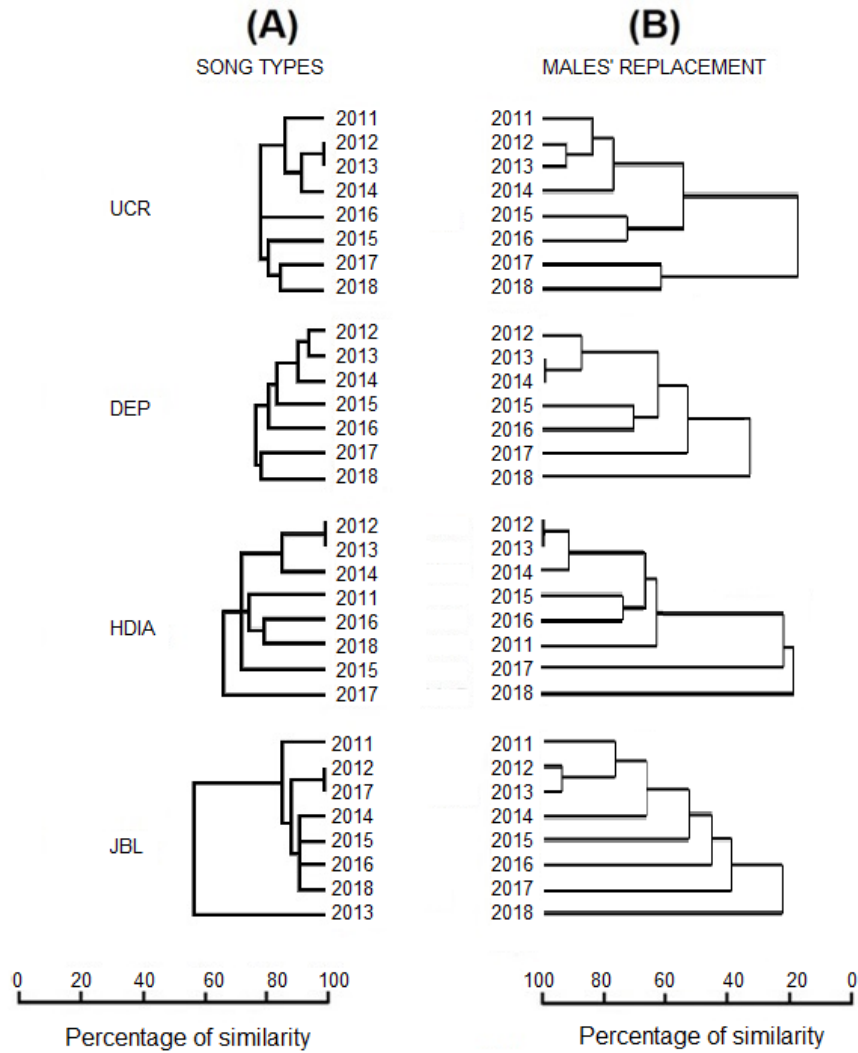


FIGURE 4 Clusters based on the Sørensen Index of similarity comparing **(A)** song types ($N = 42$ song types) in males' repertoire of White-eared ground-sparrows between years, and **(B)** males' identity ($N = 96$ males) in different years. The letters next to the branches represent each population sampled (UCR: Universidad de Costa Rica campus; DEP: Instalaciones Deportivas of the university; HDIA: north of Heredia; JBL: Jardín Botánico Lankester). When years are clustered at the end of the branches, it means they show similar patterns of repertoire use and male's replacement these years.

The probability of the common song T18 in UCR population and the less-common T44 in JBL population to remain in their respective population increased throughout the years (Figure 5; Table 3). The probability of the other song types (common and less-common) of remain in a population did not change over time (Figure 5; Table 3). The binomial test showed for most years, that the frequency of use of song types correlated positively with the frequency of their use in the previous year. The frequency of use of a specific song type increased in a year if in the previous year it had been commonly sung, and decreased if in the previous year was not commonly sung (Supplementary Material Table S1).

TABLE 3. Linear regressions testing the probability of permanence of the common and less- song types in four populations of White-eared Ground-Sparrows in Costa Rica through years.

Population	Type of song	R ²	t	P-value
UCR	14	0.384	1.767	0.138
	18	0.823	4.823	0.005
	16	0.270	-1.359	0.232
	32	0.113	0.797	0.462
DEP	13	0.597	2.432	0.072
	35	0.319	-1.369	0.243
	37	0.150	0.839	0.449
	38	0.167	-0.896	0.421
HDIA	2	0.062	0.572	0.592
	3	0.437	1.969	0.106
	1	0.0285	-0.383	0.717
	29	0.117	-0.815	0.452
JBL	21	0.218	-1.179	0.291
	42	0.195	1.102	0.321
	12	0.319	-1.532	0.186
	44	0.569	2.569	0.050

P-values in bolt mean probability statistically significant ($P < 0.05$).

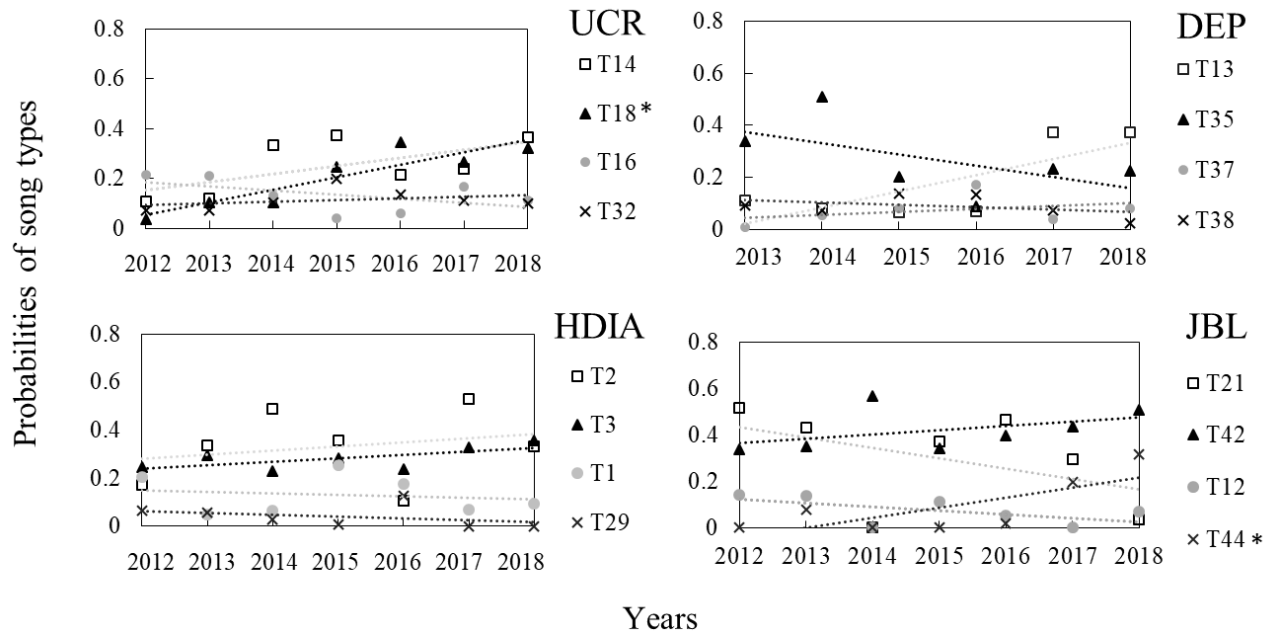


FIGURE 5 Probabilities of permanence for common and less-common song types in four populations of White-eared Ground-Sparrows in Costa Rica. Dotted lines represent timeline adjusted to linear regression. DEP: Instalaciones Deportivas of Universidad de Costa Rica; UCR: Universidad de Costa Rica main campus; HDIA: Getsemaní Heredia; JBL: Jardín Botánico Lankester.

DISCUSSION

Microgeographic variation

White-eared Ground-Sparrows had characteristic solo song repertoires that varied in magnitude across populations, separated from 30 km and 0.7 km. This confirms microgeographic song variation in this species. The White-eared Ground-Sparrows is an example of a Neotropical sparrow with song microgeographic variation as occurs in several temperate sparrows such as: Puget Sound White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*, Nelson et al. 2004), Nuttall's White-crowned Sparrows

(*Zonotrichia leucophrys nuttalli*, (Bell et al. 2003), and Savannah Sparrows (*Passerculus sandwichensis*, (Bradley 1994, Burnell 1998). In a two-year study of songs similarities in White-eared Ground-Sparrows found that males recorded in the same population share similar patterns in the use of repertoire composition in comparison to males from other populations (Sandoval et al. 2014b). I found in the present study that the solo song repertoire not only was different between populations, but also remained similar through time. Although new song types were introduced into each population each year by new arriving individuals, similarities were higher than 60 % between consecutive years within populations.

Cultural transmission influences the stability of microgeographic variation from generation to generation (Gibbs 1990, Luther and Baptista 2010), but the mechanisms that allow some songs to go extinct and others to survive are variable (Luther and Baptista 2010). Two hypotheses most likely explain how song repertoire evolved within populations: the sexual selection hypothesis, where females select males with particular song types, allowing such songs survive between years and be copied for other individuals (Darwin 1871), and also the acoustic adaptation hypothesis that states that songs that are better transmitted inside habitat characteristics survive more (Tubaro and Segura 1994). Other hypotheses tested are the demographic success hypothesis that states that song survival is related to individuals survival that sing that particular song (Gibbs 1990), the song template hypothesis that state that birds can learn new songs after 50 days using a social tutor from their new territories (Thorpe 1958, Baptista and Petrinovich 1984), and the dispersal hypothesis where arriving individuals introduce new songs (Baker and Mewaldt 1978).

Song survival

In White-eared Ground-Sparrows microgeographic song variation appears to be caused by demographic success of males. I found that the frequency with which a song is used influenced how commonly that song type will be used the next year (demographic success hypothesis), but the frequency of use did not influence if the song remains or not in the population throughout the years. This because, both common and less-common song types sung in each studied population had similar probability to be maintained through time. This pattern is different to that reported in Medium Ground Finches (*Geospiza fortis*), where the most common song type at the start of a long term study declined significantly over a six-year period, because males with less-common songs survived longer and produced more yearling offspring changing song types proportions over time (Gibbs 1990).

White-eared Ground-Sparrows have common song types, because these are better adapted for transmission or are preferred by females in each population, according to the sexual selection (Konishi 1965, Baker and Cunningham 1985) and acoustic adaptation hypothesis (Boncoraglio and Saino 2007). These two hypotheses are not mutually exclusive and explain why common song types remained common throughout time, which has been reported in other sparrow species. For example, in White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) females respond more strongly to local common songs than to alien species songs promoting that local songs survive throughout time (Baker et al. 1982). In Rufous-collared Sparrows (*Zonotrichia capensis*, (Tubaro and Segura 1994) and White-crowned Sparrows (Luther and Baptista 2010) song survival is associated with the acoustic characteristics of songs, which allow more effective communicated in the local

environment because songs are adapted to it. Another explanation to understand the long song survival in White-eared Ground-Sparrows is that new individuals arriving to the population imitate local songs (as I present here) to facilitate interactions with the new social group, as occurred in juveniles of Yellow-naped Amazons (*Amazona auropalliata*, Salinas-Melgoza and Wright 2012).

In addition to the microgeographic song variation produced by demographic success, the local replacement of males in the population was also a factor that determines the repertoire composition each year. In DEP, UCR and HDIA population where male replacement was lower than in JBL, song repertoire composition was also similar throughout time. This indicates that microgeographic song variation is not only affected by new conspecific arrivals through time, but likely influenced by other song selective forces as habitat features.

I found that some new individuals brought new songs to the population, but they also produced the most common song in each one, supporting the song template and dispersal hypotheses (Baptista and Petrinovich 1984, Graham et al. 2017) to explain the microgeographic song variation between populations. When populations are sedentary, natal and breeding territories are closer, consequently young males acquire their song repertoire in the same area that they establish as adults, increasing the similarities of the song repertoire (Lemon 1975, Krebs and Kroodsma 1980, Baker and Cunningham 1985). Alternatively, when males disperse far from natal territories, microgeographic song variation could occur because they acquired their song repertoire in the breeding territories from their neighbors (Kroodsma et al. 1982, Baker and Cunningham 1985). In this case, the capacity to learn and acquire new song must persist until they establish in their new

population (Baker and Cunningham 1985). Given that White-eared Ground-Sparrows disperse far from natal territories (Sandoval et al. unpub. data), microgeographic song variation can give us a clue about where they learn to sing and how differences in repertoire are maintained between populations, under the expectations of the song template hypothesis (Nordby et al. 1999).

New song arrives

In our study, I found new song types with elements structurally different from common songs in new males arriving to the population each year, suggesting that they learned those songs in the natal territory before dispersal, because new males had different song types between them. But, after establishing a territory, the new males shared common songs of the population, suggesting that males learned those songs after arriving, supporting the vocal imitation hypothesis (Salinas-Melgoza and Wright 2012). This pattern of song learning has been reported in banded juveniles of South Island Saddleback (*Philesturnus carunculatus*, Jenkins 1978) and Indigo Buntings (Payne 1981, 1982) that disperse and learn songs in their new territories.

Another mechanism that induces cultural change in songs is mutation: individual differences are produced by improvisations during the process of song development that produces a novel recombination of learned song or a completely new song (Hultsch and Todt 2004, Marler and Slabbekoorn 2004, Brenowitz and Beecher 2005, Catchpole and Slater 2008). I found these cultural mutations in White-eared Ground-Sparrows songs in DEP and UCR populations: recombination of common songs to create new song types (Supplementary Material Figure S1) and improvisation as pointed mutations, adding new elements to common song types (Supplementary Material Figure S2).

Conclusion

White-eared Ground-Sparrows have microgeographic song variation in a scale of less than 1 km displaying song repertoires shared by members of a local population. The microgeographic song variation showed stability and persistence through time. This variation was explained by replacement of males, but little explained by the frequency of use of song types. I suggest that these ground-sparrows learn their song mainly in their breeding territories from their breeding neighbors, due to the patterns in song variation, and they can introduce new songs from their natal territories as they disperse to new populations. More studies are necessary to understand their vocal learning, if it is this an open-ended or closed-ended learner. In addition, it would be important to describe boundaries in the song variation between continuous populations and to define the area of these groups. In this study, I settled the basis for cultural transmission and variation in male solo song in a Neotropical sparrow.

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SUPPLEMENTARY MATERIAL TABLE S1. Probabilities of common types of songs in four populations of White-eared Ground-Sparrows in Costa Rica.

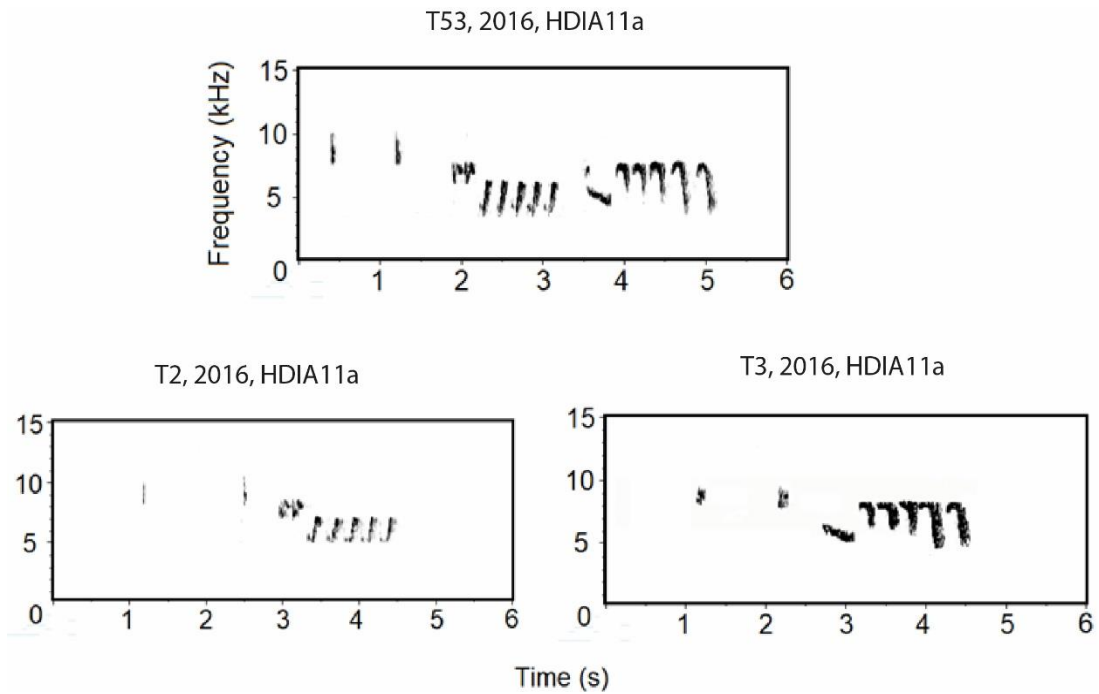
Population	Type of song	Year comparison	Observed songs	Total observations	Expected probability	P-value Binomial	Percentage of success
UCR	T14	2011-2012	23	158	0.108	0.032	100
		2012-2013	73	219	0.122	< 0.001	
		2013-2014	95	243	0.122	< 0.001	
		2014-2015	48	223	0.333	< 0.001	
		2015-2016	17	71	0.375	0.006	
		2016-2017	114	284	0.215	< 0.001	
		2017-2018	129	358	0.239	< 0.001	
	T18	2011-2012	20	158	0.038	< 0.001	85.7
		2012-2013	23	219	0.106	0.087	
		2013-2014	63	243	0.105	< 0.001	
		2014-2015	77	223	0.249	< 0.001	
		2015-2016	19	71	0.345	0.039	
		2016-2017	100	284	0.268	< 0.001	
		2017-2018	138	358	0.322	0.002	
	T16	2011-2012	40	158	0.215	0.037	100
		2012-2013	29	219	0.213	0.001	
		2013-2014	10	243	0.132	< 0.001	
		2014-2015	14	223	0.040	0.028	
		2015-2016	12	71	0.063	0.001	
		2016-2017	35	284	0.169	0.007	
		2017-2018	33	358	0.113	0.033	
	T32	2011-2012	14	158	0.073	0.086	42.9
		2012-2013	23	219	0.074	0.023	
		2013-2014	50	243	0.105	< 0.001	
		2014-2015	30	223	0.198	0.004	
		2015-2016	8	71	0.135	0.127	
		2016-2017	31	284	0.113	0.074	
		2017-2018	34	358	0.100	0.068	
DEP	T13	2011-2012	30	365	0.112	0.012	83.3
		2013-2014	43	647	0.082	0.020	
		2014-2015	23	327	0.064	0.077	
		2015-2016	90	242	0.070	< 0.001	
		2016-2017	105	257	0.372	0.024	
		2017-2018	131	468	0.374	< 0.001	
	T35	2011-2012	186	365	0.337	< 0.001	83.3
		2013-2014	137	647	0.510	< 0.001	
		2014-2015	29	327	0.203	< 0.001	
		2015-2016	56	242	0.089	< 0.001	
		2016-2017	63	257	0.231	0.051	
		2017-2018	102	468	0.224	0.042	

HDIA	T38	2011-2012	26	365	0.092	0.030	83.3	
		2013-2014	94	647	0.071	<0.001		
		2014-2015	44	327	0.139	0.062		
		2015-2016	18	242	0.135	0.001		
		2016-2017	7	257	0.074	<0.001		
		2017-2018	36	468	0.025	<0.001		
	T40	2011-2012	20	365	0.009	<0.001	83.3	
		2013-2014	54	647	0.055	<0.001		
		2014-2015	56	327	0.080	<0.001		
		2015-2016	9	242	0.171	<0.001		
		2016-2017	23	257	0.037	<0.001		
		2017-2018	41	468	0.082	0.059		
	HDIA	T2	2011-2012	288	717	0.170	<0.001	100
			2012-2013	165	338	0.337	<0.001	
2013-2014			180	485	0.337	0.011		
2014-2015			45	423	0.488	<0.001		
2015-2016			189	356	0.356	<0.001		
2016-2017			140	384	0.106	<0.001		
2017-2018			322	580	0.531	0.017		
T3		2011-2012	251	717	0.246	<0.001	100	
		2012-2013	78	338	0.294	0.002		
		2013-2014	143	485	0.231	<0.001		
		2014-2015	101	423	0.283	0.005		
		2015-2016	117	356	0.239	<0.001		
		2016-2017	150	384	0.329	0.003		
		2017-2018	223	580	0.357	0.013		
T23		2011-2012	42	717	0.205	<0.001	100	
		2012-2013	22	338	0.049	0.038		
		2013-2014	129	485	0.065	<0.001		
		2014-2015	74	423	0.255	<0.001		
		2015-2016	25	356	0.175	4.E-09		
		2016-2017	40	384	0.070	0.003		
		2017-2018	34	580	0.095	<0.001		
T29		2011-2012	47	717	0.064	0.060	57.1	
		2012-2013	10	338	0.055	0.010		
		2013-2014	4	485	0.030	<0.001		
	2014-2015	54	423	0.008	<0.001			
	2015-2016	0	356	0.128	<0.001			
	2016-2017	0	384	0.000	1			
	2017-2018	0	580	0.000	1			
JBL	T42	2011-2012	173	400	0.516	<0.001	85.7	
		2012-2013	0	4	0.433	0.104		
		2013-2014	137	308	0.000	0		
		2014-2015	97	208	0.371	0.001		
		2015-2016	43	146	0.466	<0.001		

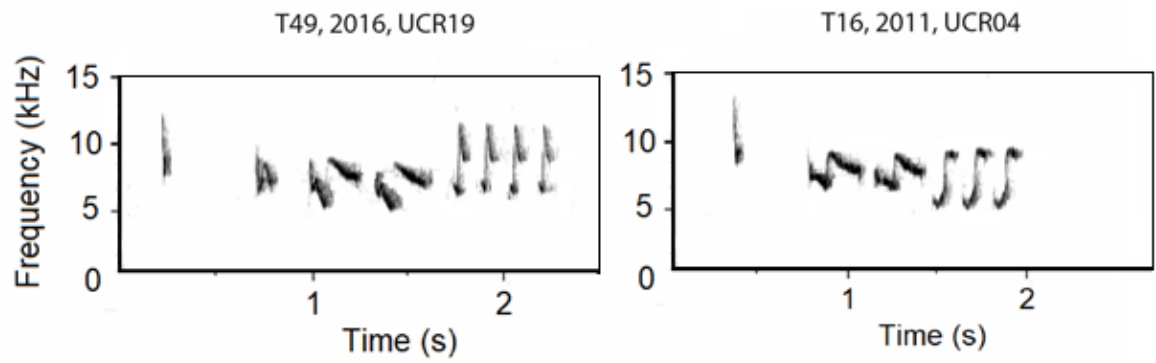
	2016-2017	2	53	0.295	<0.001	
	2017-2018	79	270	0.035	<0.001	
T21	2011-2012	141	400	0.340	0.037	85.7
	2012-2013	3	4	0.353	0.113	
	2013-2014	127	308	0.569	<0.001	
	2014-2015	83	208	0.344	0.014	
	2015-2016	64	146	0.399	0.042	
	2016-2017	29	53	0.438	0.031	
	2017-2018	94	270	0.510	<0.001	
T12	2011-2012	55	400	0.144	0.054	71.4
	2012-2013	0	4	0.138	0.553	
	2013-2014	42	308	0.000	0	
	2014-2015	11	208	0.114	0.001	
	2015-2016	0	146	0.053	<0.001	
	2016-2017	4	53	0.000	0	
	2017-2018	47	270	0.070	<0.001	
T44	2011-2012	31	400	0.000	0	85.7
	2012-2013	0	4	0.078	0.724	
	2013-2014	1	308	0.000	0	
	2014-2015	4	208	0.003	0.002	
	2015-2016	29	146	0.019	<0.001	
	2016-2017	18	53	0.199	0.006	
	2017-2018	47	270	0.317	<0.001	

P-values in bolt mean probability statistically significant ($P < 0.05$). Percentage of success

means the percentage of cases statistically significant for each song type.



SUPPLEMENTARY MATERIAL FIGURE S1. Example of recombination in solo song types of White-eared Ground-Sparrows as consequence of song learning by imitation. T53 was a recombination from common song types T2 and T3.



SUPPLEMENTARY MATERIAL FIGURE S2. Example of improvisation in solo song types of White-eared Ground-Sparrows as consequence of song learning by imitation. An additional element was integrated in T49 from the original T16.