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REVEALING A COMPLEX PATTERN OF SONG VARIATION IN *Zonotrichia capensis australis* IN EASTERN PATAGONIA

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ABSTRACT: The Patagonian subspecies of the Rufous-collared Sparrow (*Zonotrichia capensis australis*) is the most morphologically distinct, lacking the typical black crown stripes. Previous studies in northeastern Patagonia had shown that songs include pretheme notes and lack a trill, but we have recently shown that this is not the case in southeastern Patagonia. In order to study vocal variation throughout eastern Patagonia, we recorded and analyzed the songs of about 500 *Z. capensis* individuals from Santa Rosa (La Pampa province) to Monte León National Park (Santa Cruz province). We detected three regiolects. The northernmost Espinal regiolect is replaced in Sierra Grande (Río Negro province) and between Punta Colorada and Puerto Lobos (Chubut province), by songs with an atypical structure, frequently including a pretheme and lacking a trill. This Northeastern Patagonia regiolect extends to approximately 100 km south of Trelew (Chubut province), where it is replaced by the Southeastern Patagonia regiolect with its more typical structure and different types of trills. Principal component analyses showed that the Northeastern Patagonia regiolect also differed significantly from the other two regiolects in the theme. In turn, the Espinal and Southeastern Patagonia regiolects differed in various trill variables. Notably, these patterns of vocal variation were decoupled from the gradual transition between the typical black-striped crowns and the gray crowns characteristic of *Z. c. australis*. Possible non-exclusive factors underlying this vocal variation, particularly the trill-less songs in northeastern Patagonia, include stochastic processes, song-learning biases, adaptation to environmental acoustics, and, most likely, differences in migratory patterns.

KEYWORDS: *acoustic adaptation, regiolects, Rufous-collared Sparrow, song dialects, vocal learning, vocal variation*

Bird song dialects are geographically distinct variants of vocalizations within a species, which result from vocal learning through imitation and therefore constitute true examples of animal culture (Mundinger 1982). Much of the initial interest in dialects, which continues to this day, is related to the possibility that they may act as barriers to gene flow between populations with different vocal traditions, promoting divergence and eventually speciation (Nottebohm 1969, Baker 1975, Lougheed & Handford 1992, 1993, Danner et al. 2017, Luo et al. 2024).

Differences among dialects could reflect the adaptation of signal design for long-range communication in environments with different acoustic characteristics (by minimizing signal attenuation and degradation, reducing acoustic masking, and/or increasing signal consistency; Wiley & Richards 1978, Richards & Wiley 1980, Brown & Handford 1996, 2000, Dooling & Blumenrath 2013, Francis et al. 2023). This is the basis of the 'Acoustic Adaptation Hypothesis' (Morton 1975). Studies across avian taxa have provided mixed support for this explanation (see reviews by Blumstein & Turner 2005, Boncoraglio & Saino 2007,

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Barker 2008, Ey & Fischer 2009, Hardt & Benedict 2021, Mikula et al. 2021), so its generality remains a matter of controversy. Nevertheless, some species, such as the Rufous-collared Sparrow (*Zonotrichia capensis*), stand out for having dialect systems closely associated with environmental characteristics.

Nottebohm (1969) first described the system of dialects of the Rufous-collared Sparrow in Argentina. Since then, this species has become a model for understanding how song variation is linked to habitat characteristics (Nottebohm 1975, Handford 1981, 1988, Lougheed et al. 1989, Tubaro et al. 1993, García et al. 2015, Tubaro et al. 2026). The song of this species is composed of two parts: a theme or introduction, comprising a variable number of whistled notes with slow frequency modulation, and a trill, which consists of the repetition of a note with a rapid descending frequency modulation (Fig. 1). The temporal separation between notes in the trill—the trill interval—is shared among individuals singing within a given area but differs among habitats, thereby defining dialects. The theme varies among individuals within the same population, defining their particular song type (although the same theme, with slight variation, can be shared by multiple individuals). These themes may differ in the number of notes, their duration, and modulation patterns. Furthermore, in some regions, they include an initial series of very brief notes with descending frequency modulation termed the 'pretheme' or 'preintroduction' (Tubaro 1990).

Several studies have shown that dialects from closed habitats such as forests and woodlands have trills with more separated notes (i.e., slower trills) compared to those from open habitats such as grasslands, savannas, and high-altitude meadows (Nottebohm 1969, 1975, Handford 1981, 1988, Lougheed et al. 1989, Tubaro et al. 1993). This is consistent with the predictions of the 'Acoustic Adaptation Hypothesis', as in closed habitats the accumulation of echoes resulting from sound reflections off branches, trunks, and leaves constitutes the main source of signal degradation. Under these conditions, trills with more separated notes reduce the likelihood that echoes from each note overlap with the beginning of the next one. In contrast, the main source of distortion in open habitats arises from random amplitude fluctuations caused by the interaction of sound with moving environmental heterogeneities (air cells in motion with varying temperature and humidity). This favors the use of trills with a high repetition rate, ensuring that at least part of the signal reaches the receiver with adequate amplitude (Wiley & Richards 1978, Richards & Wiley 1980). In addition, a high rate of note repetition increases communication consistency in open areas (Brown & Handford 1996, 2000). Although the association between trill interval and habitat in this species is generally consistent with the predictions of the 'Acoustic Adaptation Hypothesis', a few exceptions have been identified, including longer trill intervals in the open Southern Pampas in Argentina compared to the closed Espinal (Tubaro & Segura 1994, Lijtmaer & Tubaro 2007) and the lack of a trill in the open Argentine Northern Monte Desert (Handford 2005).

Song dialects of *Z. capensis* occur at different spatial scales, as they may be either macrogeographic or microgeographic. For example, throughout the Pampas region, songs have trill intervals in the range of 60–70 ms (Nottebohm 1969, 1975), whereas the Magdalena Talar dialect occupies a narrow strip, only a few hundred meters wide, extending for a few kilometers along the coast of the Río de la Plata, with trill intervals of 90–120 ms (Tubaro et al. 1993, Kopuchian et al. 2004, García et al. 2015). Transitions between dialects may also be abrupt (as in the transition between the Southern Pampas and Espinal dialects; Tubaro & Segura 1994, Lijtmaer & Tubaro 2007) or gradual. In the latter case, the gradual change is associated with the presence of ecotones, as in the case of the Talar dialect and the surrounding Pampas Steppe dialect (Tubaro et al. 1993), or between the lowland Pampas Steppe and the Tandil, Balcarce, and Ventania mountain ranges (Nottebohm 1975).

In the context of song variation in the Rufous-collared Sparrow, Patagonia is particularly interesting because, at least in its northeastern area, songs are quite atypical, including a pretheme and no trill (Hudson 1920, King 1974, Nottebohm 1975, Handford 2005). In addition, the Patagonian subspecies *Z. c. australis* is the most differentiated morphologically, as it lacks the black stripes on the crown, a trait that has been recently shown to be the consequence of genomic differences affecting the expression of a specific gene related to melanin production (Lavinia et al. 2025). However, these features of *Z. c. australis* appear not to be homogeneous throughout Patagonia. For instance, in a recent study conducted in Monte León National Park, in southeastern Patagonia, we have shown that *Z. capensis* songs have a typical structure, with a theme and a trill, and with the presence of microgeographic patterns of dialectal variation that resemble those found in other regions of Argentina (Tubaro et al. 2026).

The contrasting results among previous studies in Patagonia could stem at least in part from differences

between the areas studied, such as northeastern vs. southeastern Patagonia, and the fact that previous vocal analyses in the region were mostly fragmented and focused on specific localities. Given that a larger-scale vocal analysis across Patagonia is needed to better understand the vocal patterns in the region, the objectives of this study were (1) to describe vocal variation along a large-scale transect in eastern Patagonia, (2) to study in detail the characteristics of the atypical songs present in northeastern Patagonia, (3) to analyze the transition between the songs of this area and those occurring to the north (Espinal) and south (southeastern Patagonia), and (4) to briefly describe the variation in plumage coloration throughout the same transect and its association with vocal variation.

METHODS

We recorded the songs of 486 spontaneously singing adult Rufous-collared Sparrows in September 2022 and between October and November 2025 (Supplementary Material Table S1). Recordings were made along an approximately 1500 km north–south (N-S) transect extending from Santa Rosa (La Pampa province) through Río Negro and Chubut provinces, and ending in Monte León National Park (Santa Cruz province). This transect encompassed the Espinal, Monte, and Patagonian Steppe ecoregions (Morello et al. 2012), as well as transition zones among them (Supplementary Material Fig. S1). All birds were recorded at short distance (5-10 m in most cases) at localities and roads that were selected to ensure an adequate sample size and even sampling coverage.

We used either a MixPre-3 digital recorder (sample rate 44.1 kHz; bit depth = 24) with a Sennheiser ME67 long shotgun microphone equipped with a K6 power unit and a Rycote Softie windscreen, or the mobile applications RØDE Rec LE v2.9.43 and Merlin (Cornell Lab of Ornithology, Ithaca, NY) on an iPhone 14 Plus (sample rate 44.1 kHz, bit depth = 16). All recordings were in uncompressed *.wav* format. To avoid sampling the same individual more than once, we followed the criterion of Nottebohm (1969), refraining from recording individuals located less than 50 m apart unless they were singing simultaneously.

All recordings were deposited in the Colección Nacional de Sonidos Naturales at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'. Since Rufous-collared Sparrows typically produce a single song type with negligible variation among successive renditions (at least in Argentina; Nottebohm 1969, 1975, King 1972), we analyzed the song with the highest signal-to-noise ratio from each individual. Spectrographic analyses were performed using Raven Pro (Cornell Lab of Ornithology, Ithaca, NY, U.S.A., version 1.6.5), with the Hann window function, a frame of 512 samples (11.6 ms), 50% overlap, 256 hop size, a 3 dB filter bandwidth of 124 Hz, and a grid spacing of 86.1 Hz. We first registered the number of notes (NN) of 1) the theme (including the pretheme), 2) the pretheme separately, and 3) the trill. We also recorded the number of notes of the theme with descending frequency modulation. The following variables were measured on each spectrogram using Raven's selection box (Fig. 1): maximum frequency (FMAX), minimum frequency (FMIN), and duration (ΔT) of both the theme and the trill. The duration of the trill was measured from the midpoint of the first trill note to the midpoint of the last one. Peak frequency (FPEAK), defined as the frequency with the most energy, and the frequencies below which 5% and 95% of the total signal energy are contained (F5% and F95%, respectively) were determined automatically by the software. These variables were $\log_{10}$ transformed for statistical analysis. This transformation helps to normalize the data and is also recommended considering the way birds produce and perceive sounds (Cardoso 2013). We also calculated the theme and the trill bandwidths, both using $\Delta F = \log_{10} FMAX - \log_{10}$

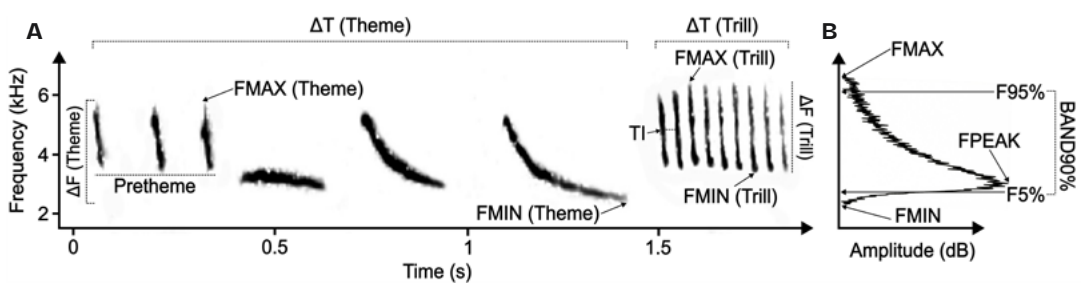

Figure 1. Spectrogram (left) and power spectrum (right) of a Patagonian *Zonotrichia capensis* song showing the variables measured. Abbreviations: FMAX: maximum frequency; FMIN: minimum frequency; FPEAK: peak frequency; ΔT: theme and trill durations; ΔF: theme and trill bandwidths; BAND90%: 90% bandwidth; TI indicates the trill interval.

FMIN and BAND90% = $\log_{10}$ F95% – $\log_{10}$ F5%. Finally, to estimate the trill interval (TI), we divided the trill duration by the number of spaces between trill notes (i.e., trill notes minus one). In a few cases where trills were very fast (i.e., buzzes), the number of notes and trill interval could not be reliably measured, and we recorded only their acoustic frequency variables and duration. It is important to note, however, that given the pulsatile nature of the sound elements composing the buzz, frequency variables are probably estimated with great uncertainty (even when increasing the FFT window size), and their values must be interpreted with caution. In rare cases in which the song contained two trills, we registered this condition but measured only the acoustic variables of the slower trill.

Due to the large geographic scale of this study, we analyzed dialects that occur over broad geographic areas and are also markedly distinct in structure (i.e., with or without a trill). We hereafter use the term 'regiolect' to refer to these large-scale dialects. Although this term has not been frequently used (but see Mundinger 1982, Pitocchelli et al. 2024), we believe it is useful to describe the vocal changes we found in the Rufous-collared Sparrow at a macrogeographic scale across the extensive Patagonian region, and to distinguish them from local variation occurring at microgeographic scales.

We analyzed the theme and the trill separately because of the aforementioned differences in their patterns of variation and because one of the regiolects lacked the trill. For both the theme and the trill, we performed a principal component analysis (PCA) to statistically compare their structure among regiolects. The PCA reduces the dimensionality of the set of variables and generates a smaller number of mutually independent variables, thus allowing for a better comparison of song structure. Each PCA was performed using the correlation matrix without rotation. We considered variables to be significantly correlated with a PC when the absolute value of their factor loading was greater than 0.7 (Tabachnick & Fidell 2007). We then performed non-parametric Kruskal–Wallis tests using the principal component scores as the dependent variables and the regiolect as the independent (grouping) variable. When significant differences among regiolects were detected, we conducted pairwise Mann-Whitney *U* tests for *post-hoc* comparisons. Data manipulation and all statistical analyses were performed using the *tidyverse* package (Wickham et al. 2019) in R version 4.5.1 (R Core Team 2025).

RESULTS

General pattern

We found a clear pattern of song variation along the study area that included one region without trills in northeastern Patagonia, hereafter referred to as the Northeastern Patagonia regiolect, bordered to the north by the Espinal regiolect and to the south by the Southeastern Patagonia regiolect, both of which had trills with varied characteristics (Figs. 2 & 3). The boundary between the Northeastern Patagonia regiolect and the fast-trilled Espinal regiolect occurred along a SE-NW diagonal across Río Negro province (Fig. 4). This transition was rather steep, starting south of Playas Doradas, meaning that most of the San Matías Gulf coast is occupied by the Espinal regiolect, with the exception of its southern part from Puerto Lobos to Punta Norte in the Valdés Peninsula (Chubut province), where *Z. capensis* sings only the theme. Toward the west and north, the songs without a trill were sung in Sierra Grande and Sierra Pailemán, reaching almost as far as Provincial Route 23 and the city of Valcheta. To the south, the Northeastern Patagonia regiolect extended to Puerto Madryn, Trelew, and Punta Tombo (in Chubut province), but south of this point the trilled songs reappeared, marking the transition to the Southeastern Patagonia regiolect, which is present at least as far south as Monte León National Park, in Santa Cruz province.

Given that the Espinal and Southeastern Patagonia regiolects were rather diverse in their characteristics across the large areas that they occupied, in the following analyses, we included only individuals located within 100 km of the boundary with the Northeastern Patagonia regiolect.

Differences among regiolects in the theme

As is typical in the Rufous-collared Sparrow, the introductory part of the song included a variable number of frequency-modulated tonal notes. The number and shape of the notes varied among individuals within the same regiolect (see Fig. 3), although neighboring individuals sometimes shared theme variants. The number of notes both in the pretheme and in the whole theme was variable but tended to be higher in the Northeastern Patagonia regiolect (Table 1). A notable feature of the themes in the study area was the predominance of notes with descending frequency modulation. This feature is typical of themes in western and southern Argentina, in contrast to those of the Pampas region, where there is a higher proportion of notes with ascending frequency modulation (Tubaro 1990, Handford & Lougheed 1991).

The Principal Component Analysis of the theme extracted four factors with eigenvalues greater than one, which together explained more than 79% of the variation in the original dataset (Table 2). PC1 represented an axis characterized by an increasing number of notes in the theme and the pretheme, as well as a wider theme bandwidth (as estimated by ΔF); the number of notes with descending frequencies and the duration of the theme also correlated positively with this PC, even though their loadings were slightly below 0.7. PC2 correlated with a decreasing bandwidth (as estimated by BAND90%) and maximum frequency (F95%). Higher PC3 scores represented lower minimum frequencies (F5%). PC4 did not have a high loading for any specific variable and was thus not readily interpretable. PC1, PC2, and PC4 scores differed among regiolects (Kruskal-Wallis test ≥ 6.17, $p \leq 0.046$). Fig. 5 illustrates the position of each song in the space determined by the first two PCs, showing a tendency of the Northeastern Patagonia regiolect to separate from the other two regiolects along PC1. Pairwise comparisons indicated that both PC1 and PC2 scores were significantly higher in the Northeastern Patagonia regiolect compared to the other two regiolects ($p < 0.001$; Table 3). This indicates that northeastern Patagonian birds had longer themes with more notes (both in the pretheme and in the theme as a whole), a higher number of notes with descending modulation, lower maximum frequencies (F95%), and narrower bandwidths. In contrast, the Espinal and Southeastern Patagonia regiolects (at least considering the songs close to the boundary with the Northeastern Patagonia regiolect) did not significantly differ from each other ($p \geq 0.073$; Table 3).

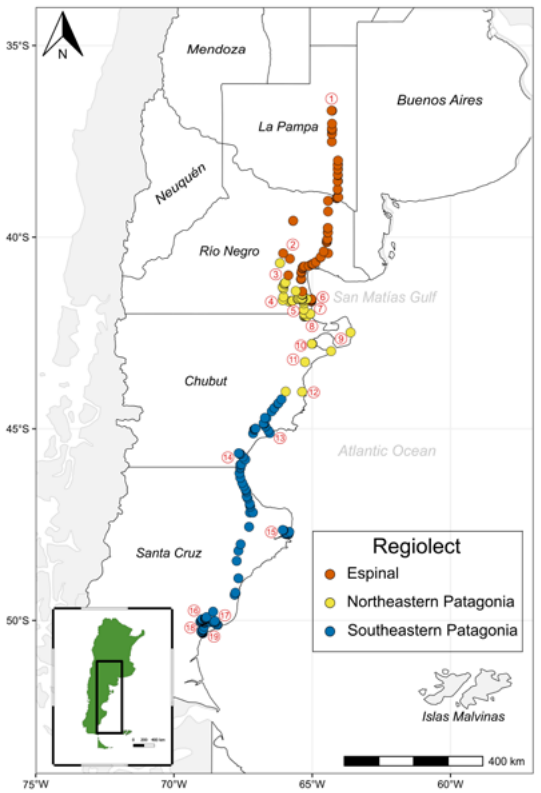

Figure 2. Sampling locations for *Zonotrichia capensis* songs along eastern Patagonia, from La Pampa province to Monte León National Park. Orange, yellow, and blue dots represent individuals that belong to the Espinal, Northeastern Patagonia, and Southeastern Patagonia regiolects, respectively. Geographic references: 1) Santa Rosa, 2) Valcheta, 3) Sierra Pailemán, 4) Pueblo Nuevo, 5) Sierra Grande, 6) Playas Doradas, 7) Punta Colorada, 8) Puerto Lobos, 9) Península Valdés, 10) Puerto Madryn, 11) Trelew, 12) Punta Tombo, 13) Bahía Bustamante, 14) Comodoro Rivadavia, 15) Puerto Deseado, 16) Santa Cruz River Valley, 17) Cañadón del Puerto Santa Cruz, 18) Cañadón de los Guanacos, and 19) Monte León National Park. The inset map displays the location of the study area within Argentina.

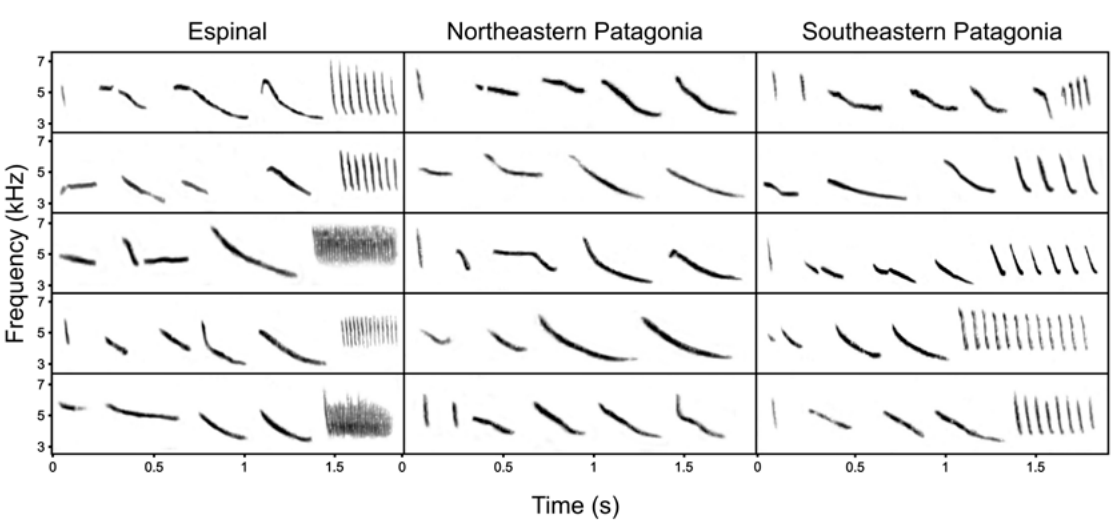

Figure 3. Representative songs of the three regiolects identified in the study area. Left: Espinal regiolect, showing the theme followed by a fast terminal trill. Center: Northeastern Patagonia regiolect, characterized by the absence of a terminal trill. Right: Southeastern Patagonia regiolect, which also has a terminal trill.

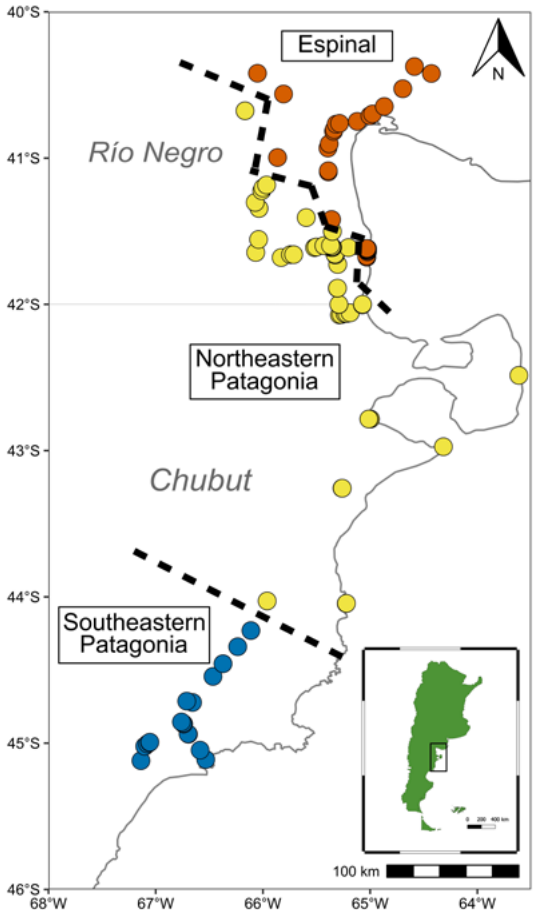

Figure 4. Sampling locations of the *Zonotrichia capensis* individuals recorded in the central portion of the study area. The map includes all individuals singing the Northeastern Patagonia regiolect (yellow dots) and the individuals singing the Espinal (orange) and Southeastern Patagonia (blue) regiolects that are closest to the boundaries between regiolects (indicated by black dashed lines). The inset map displays the location of this area within Argentina.

Differences among regiolects in the trill

For this analysis, we compared the Espinal and Southeastern Patagonia regiolects, as the Northeastern Patagonia regiolect does not include a trill. The first three factors of the PCA had eigenvalues greater than one and accounted for more than 82% of the total variance of the original dataset (Table 2). PC1 varied positively with minimum frequency (both FMIN and F5%) and negatively with bandwidth (both ΔF and BAND90%) and trill interval. PC2 corresponded to an axis of increasing maximum frequency (both FMAX and F95%). Finally, PC3 represented an axis of decreasing peak frequency, although its loading was slightly below 0.7 (Table 2). PC1 and PC3 scores were significantly higher in the Espinal regiolect compared to the Southeastern Patagonia regiolect (Mann-Whitney $p \leq 0.007$; Fig. 6, Table 3), indicating that the former had higher minimum frequencies, lower peak frequencies, narrower bandwidths and faster trills.

Even though the trills of the Espinal regiolect are, on average, much faster than those of the Southeastern Patagonia regiolect, both of them exhibit considerable variation in their trill intervals. This becomes apparent when the entire transect is considered, including the birds recorded farther from the boundaries with the Northeastern Patagonia regiolect (Fig. 7). Variation is notable at some locations, especially in southeastern Patagonia, resulting from microgeographic patterns of song variation similar to those recently described at Monte León National Park (Tubaro et al. 2026).

Relationship between song features and plumage

Although more than twenty subspecies have been described throughout the extensive distribution of the Rufous-collared Sparrow (Chapman 1940, but see Handford 1985), *Z. c. australis* from Patagonia is the most morphologically distinct, as it is characterized by the absence of the typical black crown stripes (and an overall paler plumage with less melanin; Lavinia et al. 2025). Based on our field observations, the disappearance of these stripes in eastern Patagonia becomes evident south of Provincial Route 23, which latitudinally bisects Río Negro province. Furthermore, at the latitude of Playas Doradas, Sierra Grande, and Pueblo Nuevo, incomplete crown stripes predominate among the recorded individuals. However, the partial disappearance of these black stripes is not associated with the loss of the trill, as we recorded individuals with this plumage phenotype singing the Espinal regiolect in Playas Doradas and the Northeastern Patagonia regiolect in Sierra Grande (Fig. 8). The complete disappearance of the black crown markings occurs farther south in eastern Chubut, well within the area occupied by the Northeastern Patagonia regiolect, and this fully gray-crowned phenotype continues southward throughout the eastern distribution of *Z. c. australis* (at least as far south as Monte León National Park), regardless of the reappearance of trilled songs in the Southeastern Patagonia regiolect south of Trelew. These observations indicate a discordant pattern of geographic variation between song and plumage color in eastern Patagonia.

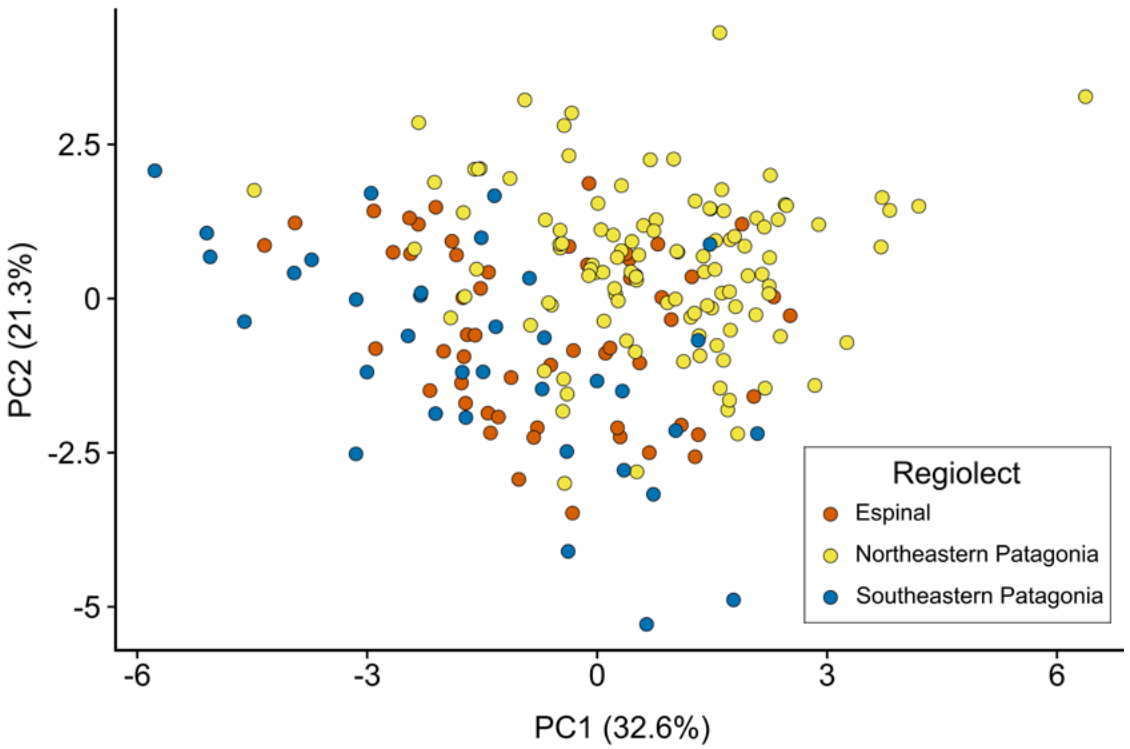

Figure 5. Distribution of the songs in the space delimited by the first two PCs of the principal component analysis (PCA) of the theme, which together explain 53.9% of the total variance. Colors represent the three regiolects: Espinal (orange), Northeastern Patagonia (yellow), and Southeastern Patagonia (blue).

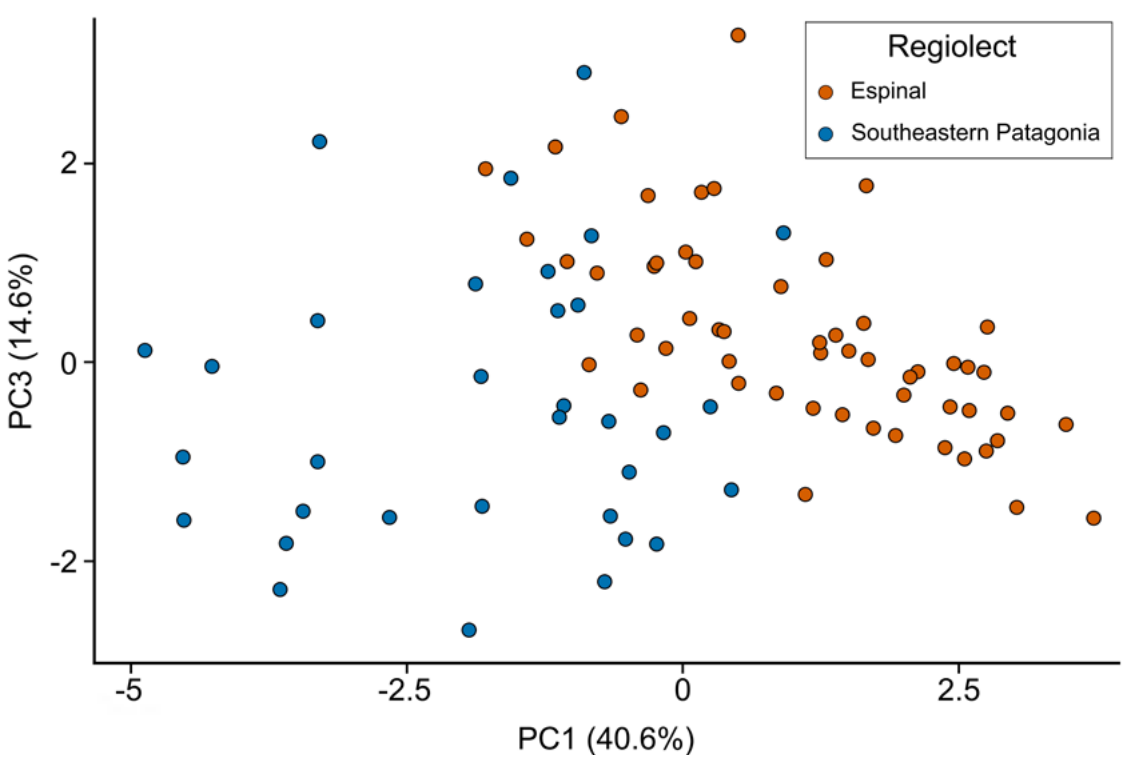

Figure 6. Distribution of the songs in the space delimited by PC1 and PC3 of the principal component analysis (PCA) of the trill, which together explain 55.2% of the total variance. Colors represent the regiolects: Espinal (orange) and Southeastern Patagonia (blue).

Table 1. Mean ± standard deviation of the theme and trill variables for the Northeastern Patagonia regiolect and the neighboring songs in the Espinal and Southeastern Patagonia regiolects (up to 100 km north and south of the boundaries depicted in Fig. 2, respectively). Frequency variables are expressed in hertz, Duration in seconds, and Trill Interval in milliseconds.
[1]Two individuals were excluded because they have very fast trills (buzzes) and their features could not be assessed properly.

	Regiolect		
	Espinal (n = 55)	**Northeastern Patagonia (n = 108)**	**Southeastern Patagonia (n = 35)**
Theme variables			
Minimum frequency (FMIN)	3101 ± 191	3057 ± 188	3151 ± 251
Maximum frequency (FMAX)	5747 ± 388	5868 ± 412	5908 ± 580
Bandwidth (ΔF)	2646 ± 441	2811 ± 444	2757 ± 725
Frequency 5% (F5%)	3596 ± 295	3585 ± 197	3615 ± 217
Frequency 95% (F95%)	5169 ± 333	5048 ± 278	5124 ± 455
Bandwidth 90% (BAND90%)	1572 ± 369	1463 ± 319	1509 ± 497
Peak frequency (FPEAK)	4556 ± 469	4431 ± 381	4496 ± 402
Duration (ΔT)	1.237 ± 0.200	1.460 ± 0.217	0.914 ± 0.259
Number of notes (NN)	4.691 ± 1.136	5.850 ± 1.226	3.514 ± 0.981
Number of notes pretheme	0.400 ± 0.627	1.513 ± 1.150	0.514 ± 0.702
Number of descending notes	4.000 ± 1.388	5.416 ± 1.771	3.257 ± 0.950
Trill variables	(*n* = 55)		(*n* = 33)[1]
Minimum frequency (FMIN)	3833 ± 350	-	3293 ± 355
Maximum frequency (FMAX)	6215 ± 398	-	6231 ± 613
Bandwidth (ΔF)	2382 ± 468	-	2939 ± 653
Frequency 5% (F5%)	4250 ± 432	-	3714 ± 359
Frequency 95% (F95%)	5610 ± 352	-	5606 ± 462
Bandwidth 90% (BAND90%)	1360 ± 380	-	1892 ± 551
Peak frequency (FPEAK)	4885 ± 599	-	4934 ± 664
Duration (ΔT)	0.336 ± 0.060	-	0.436 ± 0.211
Number of notes (NN)	12.636 ± 5.212	-	6.152 ± 6.695
Trill interval (TI)	30 ± 20	-	140 ± 90

Table 2. Factor loadings, eigenvalues, and variance explained by each principal component of the PCAs performed on theme and trill variables. Values in bold indicate factor loadings with an absolute value > 0.7.

Variable	Theme				Trill		
	PC1	PC2	PC3	PC4	PC1	PC2	PC3
Minimum frequency (FMIN)	-0.566	0.075	-0.557	-0.231	**0.940**	-0.119	-0.158
Maximum frequency (FMAX)	0.589	-0.461	-0.280	0.443	0.197	**0.878**	-0.047
Bandwidth (ΔF)	**0.775**	-0.377	0.147	0.462	**-0.737**	0.608	0.116
Frequency 5% (F5%)	-0.329	0.191	**-0.759**	0.444	0.924	-0.049	-0.287
Frequency 95% (F95%)	0.197	**-0.767**	-0.470	-0.122	0.258	**0.845**	-0.340
Bandwidth 90% (BAND90%)	0.406	**-0.748**	0.209	-0.434	-0.770	0.552	0.085
Peak frequency (FPEAK)	-0.060	-0.416	-0.486	-0.380	0.289	0.396	-0.687
Duration (ΔT)	0.688	0.330	-0.160	-0.080	-0.453	-0.522	-0.398
Number of notes (NN)	**0.761**	0.442	-0.190	-0.165	0.548	0.145	0.515
Number of notes pretheme	**0.724**	0.325	-0.232	-0.040	-	-	-
Number of descending notes	0.649	0.459	-0.176	-0.334	-	-	-
Trill interval (TI)	-	-	-	-	-0.704	-0.296	-0.565
Eigenvalues	3.583	2.340	1.635	1.155	4.062	2.712	1.460
% Variance explained	32.570	21.270	14.870	10.500	40.620	27.120	14.600

Table 3. Pairwise *post-hoc* comparisons (Mann-Whitney U tests) for the Principal Components of the PCA. For the theme, the table includes the Principal Components that differed significantly among regiolects according to the Kruskal-Wallis test. For the trill, because only two regiolects were compared, the table includes all PCs. The *U* statistic, the adjusted *Z*-score, and the Holm-adjusted *p* values are reported. Significant differences (adjusted $p < 0.050$) are highlighted in bold.

	PC	Comparison	*U*-statistic	Z_{adj}	p_{adj}
Theme	PC1	Espinal vs. Northeastern Patagonia	1591	5.124	**< 0.001**
		Espinal vs. Southeastern Patagonia	1178	1.779	0.075
		Northeastern Patagonia vs. Southeastern Patagonia	3183	5.438	**< 0.001**
	PC2	Espinal vs. Northeastern Patagonia	1828	4.323	**< 0.001**
		Espinal vs. Southeastern Patagonia	1090	1.051	0.293
		Northeastern Patagonia vs. Southeastern Patagonia	2955	4.409	**< 0.001**
	PC4	Espinal vs. Northeastern Patagonia	2939	0.568	0.570
		Espinal vs. Southeastern Patagonia	690	2.251	0.073
		Northeastern Patagonia vs. Southeastern Patagonia	1483	2.229	0.073
Trill	PC1	Espinal vs. Southeastern Patagonia	1671	6.576	**< 0.001**
	PC2	Espinal vs. Southeastern Patagonia	771	1.172	0.241
	PC3	Espinal vs. Southeastern Patagonia	1223	2.715	**0.007**

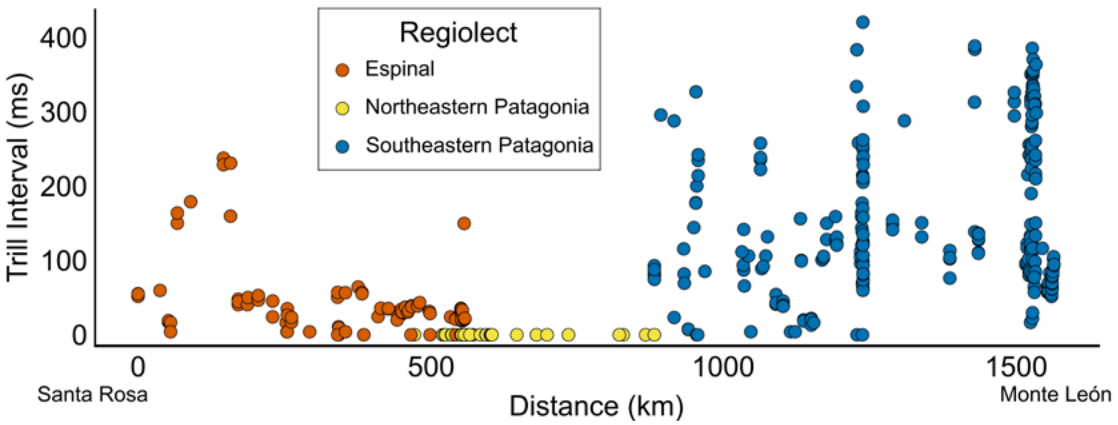

Figure 7. Trill interval (TI) along a latitudinal transect from Santa Rosa (La Pampa province) to Monte León National Park (Santa Cruz province). Colors indicate the Espinal (orange), Northeastern Patagonia (yellow), and Southeastern Patagonia (blue) regiolects. Note the absence of a trill in the Northeastern Patagonia regiolect (TI = 0 ms) and the high TI variability at certain points in both the Espinal and especially the Southeastern Patagonia regiolects.

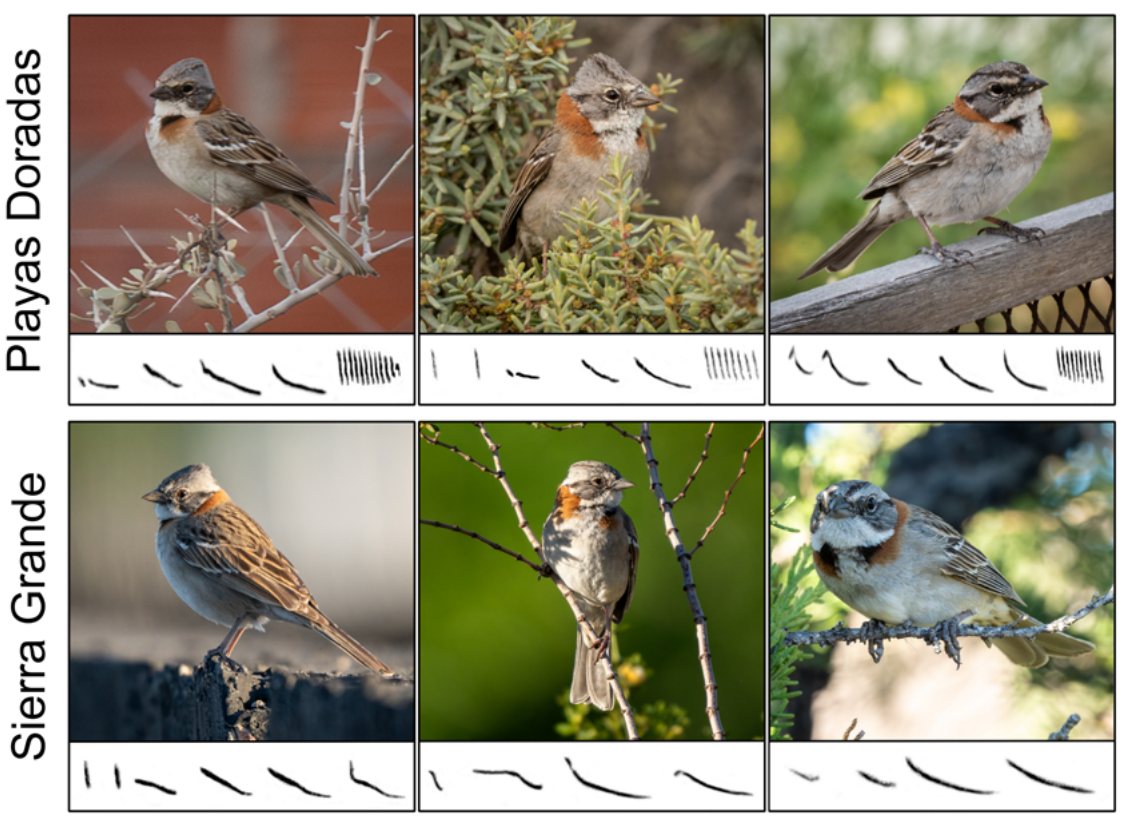

Figure 8. Photographs and corresponding schematic song structures of individuals from the transition zone. Top: three individuals from Playas Doradas exhibiting variation in the presence of black crown stripes, all singing the Espinal dialect (trilled song). Bottom: three individuals from Sierra Grande displaying similar plumage variability but singing the Northeastern Patagonia regiolect (trill-less songs). Photographs by AIC.

DISCUSSION

We presented the first detailed, large-scale study of Rufous-collared Sparrow song variation along eastern Patagonia, revealing the existence of three distinct regiolects: one in the Espinal, another in northeastern Patagonia, and a third in southeastern Patagonia. In particular, we confirmed the absence of a trill in northeastern Patagonia, in contrast to the other two trilled regiolects. Our grouping of the eastern Patagonian songs into these three regiolects was based on the presence or absence of the trill in songs from geographically coherent areas. Therefore, songs were assigned to each of these regiolects based on an objective, categorical characteristic that precludes decisions relying on subtle song differences. It is worth mentioning that although song dialects in this (and other) species have usually been defined based on observed song differences, in some cases such differences have been later on shown to also be perceived by the birds and may therefore have biological significance (e.g., Williams et al. 2019, Fracas et al. 2023, Volle et al. 2024). In particular, this has been shown in the Rufous-collared Sparrow by the differential responses of males to playback experiments using songs without trills from northeastern Patagonia and songs containing trills (Tubaro 1990). We still do not know whether this ability to perceive the difference between songs with and without trills and its effect on Rufous-collared Sparrow behavior can act as a mechanism restricting gene flow among different dialects/regiolects. Previous studies indicate that the patterns of genetic variation in this species are not concordant with the patterns of song variation either in Argentina (Nottebohm & Selander 1972, Handford & Nottebohm 1976, Lougheed & Handford 1992, 1993) or at a continental scale (Lougheed et al. 2013, Campagna et al. 2014), but more subtle effects might be detected only with detailed, genomic studies that are currently underway.

The two trilled regiolects exhibit a wide range of trill variation. In the case of the Espinal regiolect, trills are typically fast but may alternate with populations exhibiting slower trills, such as for example those in contact zones with the southern Pampas grasslands (Tubaro & Segura 1994, Lijtmaer & Tubaro 2007). Even more striking are the patterns of trill variation found within the Southeastern Patagonia regiolect, where changes in trill interval exceeding 100 ms can occur over just a few hundred meters. A microgeographic pattern of this type was recently documented in Monte León National Park (Tubaro et al. 2026), and in this study, we extended this finding to several additional localities in Santa Cruz and Chubut provinces, including Cañadón de los Guanacos, Cañadón del Puerto de Santa Cruz, the Santa Cruz River Valley, the Puerto Deseado estuary, Bahía Bustamante, and Comodoro Rivadavia (detailed analyses of these microgeographic patterns are underway).

The boundaries between the regiolects also represent areas of steep song change. These transitions, however, constitute a different phenomenon from that described above, as they involve the contact between two markedly distinct song traditions (the trill-less Northeastern Patagonia regiolect and the trilled Espinal and Southeastern Patagonia regiolects), rather than variation among structurally similar trilled songs. The northern boundary (between the Northeastern Patagonia and Espinal regiolects) is relatively abrupt and runs diagonally in a SE-NW direction from the coast of the San Matías Gulf (between Playas Doradas and Puerto Lobos) toward Sierra Grande and Sierra Pailemán. The southern boundary (between the Northeastern and Southeastern Patagonia regiolects) lies south of Punta Tombo and may extend along the coast as far as Bahía Bustamante; however, current sampling density in this area is insufficient to confirm this.

The limit between the Northeastern Patagonia and Espinal regiolects approximately coincides with the region where the black crown stripes characteristic of *Z. capensis* begin to disappear, transitioning into the gray-crown typical of *Z. c. australis* to the south. Nevertheless, there appears to be no correspondence between plumage and song phenotypes, as individuals with incomplete crown stripes in Playas Doradas sing Espinal trills, whereas 10 km to the west toward Sierra Grande, individuals with the same plumage phenotype sing the trill-less songs of the Northeastern Patagonia regiolect. Farther south, in Chubut province, fully gray-crowned individuals also sing trill-less songs, which are replaced ever farther south by the trilled songs of the Southeastern Patagonia regiolect, further demonstrating the absence of a specific association between plumage coloration and vocal phenotypes.

Because the presence or absence of the black crown stripes has a genetic basis (Lavinia et al. 2025), the lack of association between vocal and color phenotypes is consistent with the aforementioned broader-scale discordance in this species between genetic and vocal variation (Nottebohm & Selander 1972, Handford & Nottebohm 1976, Lougheed & Handford 1992, 1993, Lougheed et al. 2013, Campagna et al. 2014). Specifically, genetic patterns (and thus

morphology, including plumage coloration) are considered to reflect deeper evolutionary history, overlaid by more recent vocal variation (Lougheed et al. 2013). This is not surprising given that vocal traits are culturally transmitted and may be subject to different sources of variation and selective factors than genetic-based characteristics (Williams 2021). Specifically in this case, Patagonian Rufous-collared Sparrows might have developed their color differences during their isolation in glacial periods around 400,000 years ago (Lavinia et al. 2025). Thus, the current transition between the typical black-striped crowns and the fully gray crowns in northeastern Patagonia corresponds to the secondary contact zone between *Z. c. australis* and other subspecies (possibly *Z. c. choraules*). The more complex vocal variation that we found, on the contrary, might have been established more recently as a consequence of other, culturally-based processes (see below).

In addition to the absence of a trill, the Northeastern Patagonia regiolect is characterized by the presence of a pretheme and a predominance of notes with descending frequencies. These attributes are not exclusive to this regiolect, however, as a pretheme is also present in some individuals from the Espinal and Southeastern Patagonia regiolects. The increase in the number of pretheme notes and descending-frequency notes is also accompanied by a decrease in minimum frequency and a subsequent increase in bandwidth. The increase in the number of pre-theme and theme notes in the trill-less Northeastern Patagonia regiolect, as well as longer introductions but shorter trills in the Espinal regiolect than the Southeastern Patagonia regiolect, results in no major differences in total song duration when the three regiolects are compared (see Table 1). This is consistent with the findings of Handford and Lougheed (1991), who noted the existence of a compensation between the duration of the introduction and the trill among dialects in northwestern Argentina.

Studies in the congeneric White-crowned Sparrow (*Z. leucophrys*) have shown that the introduction and the final trill of the song have different patterns of variation and may serve different communicative functions (Nelson & Poesel 2007, Nelson et al. 2016). This is consistent with the variation present in *Z. capensis*, with themes varying notably between individuals within each dialect but trills differing mostly among dialects (Nottebohm & Selander 1972, Handford & Lougheed 1991). In particular, the Alerting Signal Hypothesis (Shiovitz 1975, Richards 1981, Ord & Stamps 2008) proposes that the structural differentiation of song constitutes an adaptation for long-distance communication in a noisy environment. According to this hypothesis, the song introduction would act as an 'alerting' element that warns potential receivers of the arrival of the informative portion of the signal. However, this hypothesis in its original form cannot explain why the informative portion of the signal would be completely lost in northeastern Patagonia. Previous playback experiments also suggest that this hypothesis may not apply to the Rufous-collared Sparrow, as males respond both to the full song and to its individual components, with similar responses to playback stimuli consisting of either the theme or the trill (Simonetti et al. 1996, Tubaro et al. 1996). This suggests that the theme also carries information and that the differences observed among regiolects could reflect the particular conditions of sound propagation in the different environments they occupy. This would be consistent with the fact that song introductions tend to propagate over greater distances and with less degradation than the trills (Handford & Lougheed 1991, Nelson et al. 2016).

There are several non-exclusive factors that could account for the singular song structure found in northeastern Patagonia, and particularly for its lack of a trill, which is an uncommon feature for this species. Below, we discuss these possible drivers and their likelihood. In the first place, we have also recently detected dialects with and without trills in the Andean region of Mendoza province (Blanco unpublished data). Given that these high-elevation populations are restricted to relatively isolated valleys, we believe that trill loss in this case may reflect stochastic processes, whereby founder effects and cultural drift could readily establish incomplete songs, a result consistent with the outcomes of neutral, stochastic song evolution in other songbirds (Baker & Jenkins 1987, Williams 2021). It has also been suggested that when populations are relatively small, elements that are more difficult to copy, such as fast trills, may be lost even if they propagate more effectively (i.e., with less degradation; Hudson & Creanza 2022). These two options, however, are more suited for small populations and would thus not be the most appropriate hypotheses to explain the lack of a trill in northeastern Patagonia due to the large number of individuals singing this regiolect. A third possibility is that trills tend to be lost because they do not propagate well in extremely windy environments. However, if this factor were decisive, trilled songs should not reappear in southeastern Patagonia, where wind is also prevalent and intense.

Finally, the difference between the Northeastern and Southeastern Patagonia regiolects could also relate to migratory behavior. Specifically, southern Patagonian *Z. c. australis* populations migrate (at least partially) toward central and northwestern Argentina, or even Bolivia, at the end of summer (Chapman 1940, King 1974, Handford 1985, Lisovski et al. 2025). There, juveniles could be exposed to the typical trilled song models during their sensitive and sensorimotor phases of vocal learning (Tubaro et al. 2026). In contrast, northeastern Patagonian populations, which are year-round residents and experience a relatively short breeding season (compared to populations in central and northern Argentina), may produce cohorts of juveniles with reduced acoustic exposure to song models, leading to the development of incomplete songs (i.e., lacking a trill). Although this remains speculative, it has been shown that contact between migratory and resident populations of the congeneric White-crowned Sparrow in the Northern Hemisphere can result in the cross-learning of elements from different dialects (Baptista 1977, Heinemann 1981). This is a particularly appealing hypothesis, because it could also explain some aspects of the decoupled patterns of variation in song and crown color in *Z. c. australis*, namely, the fact that birds singing the southern Patagonian regiolect have the typical species song structure with a trill but still possess the particular Patagonian crown pattern without the black stripes. Under this hypothesis of the effect of migration, one can explain this decoupling because even though juveniles might be exposed to the typical song structure outside Patagonia during their sensitive and sensorimotor phases of vocal learning, this cannot affect their color pattern if they reproduce only in southern Patagonia and this contact occurs in the non-breeding season.

Final remarks

The analysis of a 1500 km transect across eastern Patagonia unveiled the presence of three different regiolects in *Z. capensis* that replace each other in a mostly N-S direction: the Espinal regiolect to the north, a central Northeastern Patagonia regiolect, and finally the Southeastern Patagonia regiolect. The Espinal and Southeastern Patagonia regiolects are typical in terms of their structure and patterns of variation, comparable to the dialects found in this species in other regions of Argentina. The Northeastern Patagonia regiolect, on the contrary, has a singular structure, including various pretheme notes and the lack of a trill. This pattern of vocal variation appears to be decoupled from that of plumage coloration, as the black crown stripes are gradually lost moving south irrespective of the trill-less regiolect present in northeastern Patagonia and the reappearance of trilled songs farther south (i.e., both regiolects were sung by birds with completely gray crowns typical of *Z. c. australis*).

Various factors could be responsible for the presence of the unusual regiolect present in Northeastern Patagonia, with the difference between the migrating southern Patagonian birds and the resident northern Patagonian populations possibly playing a relevant role. Specific studies would be needed to disentangle the roles and relative significance of these factors, including (1) the analysis of isolation among populations close to the boundaries between these regiolects to understand how these relatively sharp limits could have originated and are maintained, (2) song learning experiments including various levels of degradation of song elements and trills of different speeds, (3) song transmission experiments to study the effect of the wind in the different areas, and (4) a more detailed assessment of the migration patterns of Patagonian populations in combination with the analysis of the timing of song learning in relation to migration.

This study exemplifies how patterns of variation within Patagonia can be more complex than usually assumed considering the sole effect of glacial cycles (Sérsic et al. 2011, Sánchez et al. 2024), especially when different characters are studied simultaneously. A larger-scale analysis incorporating vocalizations, more detailed crown color information, and genomic data throughout Patagonia is underway to better understand the complex evolutionary history and patterns of variation within *Z. c. australis*.

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USE OF ARTIFICIAL INTELLIGENCE

During the development of this research, artificial Intelligence was employed only to assist in the organization and structuring of the R scripts used for statistical analyses and figure preparation. During the preparation of the manuscript, it was used to improve the grammar and phrasing of specific sentences.

SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link https://doi.org/10.56178/eh.v41i2.1544.

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