



## Temporal stability and change in a microgeographical pattern of song variation in the rufous-collared sparrow

CECILIA KOPUCHIAN\*, DARIO ALEJANDRO LIJTMAER\*, PABLO LUIS TUBARO\* & PAUL HANDFORD†

\*División Ornitología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'

†Department of Biology, University of Western Ontario

(Received 20 May 2003; initial acceptance 14 August 2003;  
final acceptance 6 October 2003; MS. number: A9615)

Available online 17 July 2004

We studied the pattern of song variation in the rufous-collared sparrow, *Zonotrichia capensis*, in the 1987 and 2000 breeding seasons in a 7-km<sup>2</sup> area covering open and closed habitats. We measured 14 quantitative song variables over a total of 390 individuals and found consistent differences between habitats in both years. In particular, songs of individuals from closed habitat sites had trills with longer trill intervals and lower frequencies than those of individuals from open habitats. This pattern of variation is interpreted as a song cline that correlates with the environmental gradient. Although this cline was stable in location and shape, it also showed several differences between years. The songs recorded during 2000 had trills with longer trill intervals and lower minimum frequencies than those recorded during 1987. Thus, this study is the first to directly document temporal changes in song variables in a *Z. capensis* population. This change would be expected if all the habitats studied were more closed in 2000 than in 1987, but we did not find obvious differences in habitat features between seasons. However, this modification of song structure is compatible with alternative explanations, such as subtle differences in habitat characteristics, changes in climatic variables, a delayed effect of a past modification of the environment and neutrality of the change.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Several avian studies have shown that interspecific differences in song structure can be partially explained by the characteristics of the habitat used by each species (Morton 1975; Richards & Wiley 1980; Wiley 1991). Moreover, various intraspecific studies found an association between song structure and habitat characteristics (e.g. *Zonotrichia albicollis*, Wasserman 1979; *Thryothorus ludovicianus*, Gish & Morton 1981; *Piranga rubra* and *P. olivacea*, Shy 1983). The rufous-collared sparrow, *Zonotrichia capensis*, provides a particularly good example of this phenomenon, because of the close association between its song dialects and the features and distribution of the habitats in which it occurs (Nottebohm 1969, 1975; Handford 1981, 1988; Loughheed et al. 1989; Handford & Loughheed 1991). The song of this species comprises two parts: an introduction and a final

portion, referred to as 'theme' and 'trill', respectively (Nottebohm 1969). The theme is usually composed of two to five whistled ascending or descending notes and the trill is composed of a succession of stereotyped steeply descending frequency sweeps. Rufous-collared sparrow dialects are defined by the rate of note delivery in the trill. This trill rate is usually expressed as the 'trill interval', the average time elapsed between the end of one note and the initiation of the next note. Although trill interval is relatively consistent between males living in a given habitat, it differs between habitats, sometimes markedly. Trill intervals are usually longer in closed (forested) areas than in open ones (Nottebohm 1969, 1975; Handford 1981, 1988). Longer trill intervals are considered adaptive for long-range communication in forests because trunks and branches generate reverberation, and notes superimpose less if they are more separated, which facilitates the decoding of the signal (Morton 1975; Wiley & Richards 1978; Brown & Handford 1996, 2000).

The temporal stability of rufous-collared sparrow dialects has been studied much less than their distribution. Comparing recordings from 1969 and 1972 with

Correspondence: C. Kopuchian, División Ornitología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina (email: [ckopuchian@macn.gov.ar](mailto:ckopuchian@macn.gov.ar)). P. Handford is at the Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada.

recordings from 1984 and 1985 from the Aconquija Mountains in northwestern Argentina, Handford (1988) concluded that the dialects in that area have been stable in shape and location for approximately 20 years. More recent observations show that the geographical patterns and habitat associations in northwestern Argentina have persisted for at least 30 years. Handford inferred a much longer stability (ca. 200 years) based on the persistence of the inferred original song dialects in areas where natural vegetation had been drastically modified by human activities. In contrast, Tubaro et al. (1993) inferred the extinction of a dialect at a site along the coast of Buenos Aires Province where original vegetation was destroyed about 50 years earlier. The difference between these results is probably a consequence of the different geographical scales at which trill variation was studied. Although these studies assessed the persistence of rufous-collared sparrow dialects over time, the temporal stability of the structure of particular dialects has not been studied in this species. In this context, we studied the temporal stability and variation of dialects at a microgeographical scale by resampling an area previously studied by Tubaro et al. (1993). In particular, our objectives were (1) to assess the maintenance of the association between dialects and habitat structure that had been described for this area by Tubaro et al. (1993) and (2) to determine whether there have been changes in song structure within each of the dialects present in the area.

## METHODS

### Study Area

The study area was situated in Estancia El Destino, Partido de Magdalena, on the northeast coast of Buenos Aires Province, Argentina (35°05' S, 57°31' W). Our study site extended 7 km inland from the Río de la Plata river and was 1 km wide. Part of this site was included in a private reserve where all the natural habitats were relatively well preserved.

We identified three distinct habitats within this area.

(1) Marsh: a seasonally flooding lowland and higher ground with grass cover adjacent to the coast of the Río de la Plata. The plant genera dominating this habitat were *Scirpus*, *Salicornia* and *Paspalum*.

(2) Talar: a mixed habitat that included strips of xeromorphic woodland separated by strips of grassland. The woodland strips were parallel to the Río de la Plata river and were wider and closer together near the marsh habitat and more separated inland, where the grasslands started to dominate the environment, forming an ecotone with the steppe. The woodland comprised several tree species, including *Celtis tala* (family Ulmaceae), *Scutia buxifolia* (family Rhamnaceae), *Jodina rhombifolia* (family Santalaceae) and *Acacia caven* (family Leguminosae), and it had dense understory vegetation.

(3) Steppe: an herbaceous open grassland dominated by the genus *Stipa*, with the presence of some bushes and essentially without trees (with the exception of some planted rows of *Eucalyptus* sp. and a few isolated *C. tala*).

Detailed descriptions of these communities can be found in Parodi (1940) and Cabrera (1949, 1976).

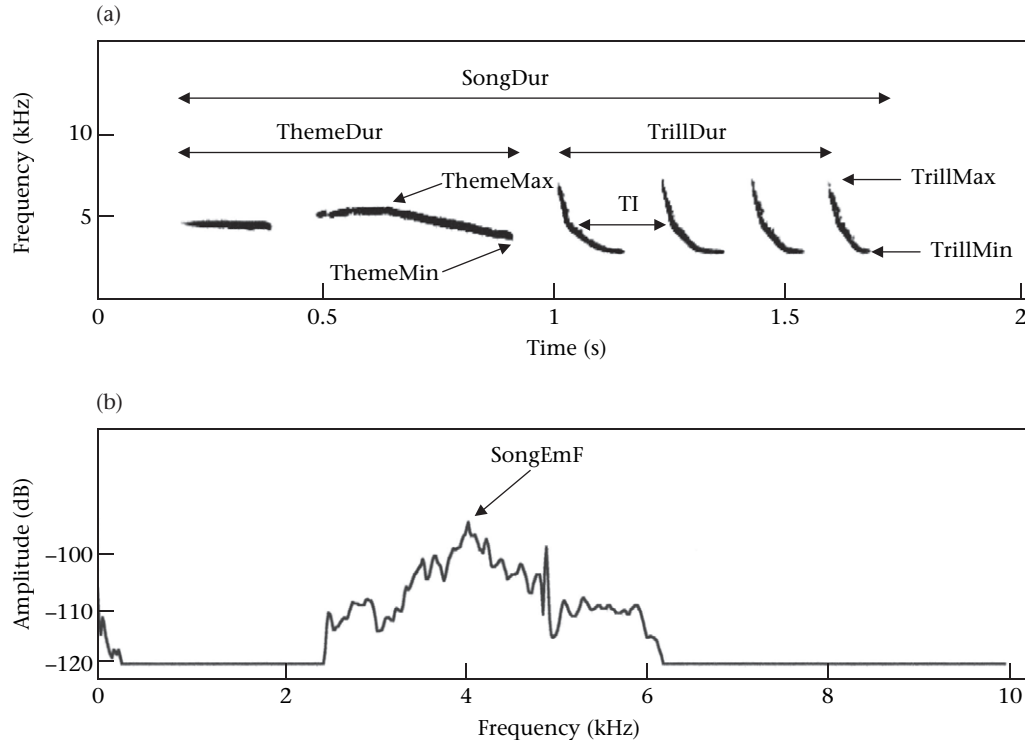
The density of rufous-collared sparrows was higher in the woodland, but the birds were abundant in all three habitats.

### Song Samples

We recorded songs of 237 and 153 rufous-collared sparrows during the 1987 (October 1987–January 1988) and 2000 (October–December 2000) breeding seasons, respectively. Recordings were performed at a speed of 9.5 cm/s, using UHER 4000 Report-L and UHER 4000 Report IC tape recorders in 1987 and 2000, respectively, and a directional cardioid Lec 980 LEEA microphone. Although wild rufous-collared sparrow singers are almost always males (King 1972), the possibility that a small fraction of the recordings correspond to females cannot be excluded because the sexes are indistinguishable. Because individuals were not banded, we avoided sampling individuals at sites closer than 50 m, with the exception of neighbours singing simultaneously (Nottebohm 1969), to ensure independence of data. Independence between the two sample years was assured because of the high turnover of rufous-collared sparrow populations (annual disappearance rate for adults ranges from 30 to 77.6%, Miller & Miller 1968; Handford 1980). Because so few birds were recorded at the marsh habitat, we pooled these data with those of the steppe into an open habitat category (excluding these data from the analyses did not change the results).

Individuals of this species usually sing only one song type and show extremely low variation between songs (Nottebohm 1969, 1975; Handford & Nottebohm 1976). Therefore, in most cases, we included only one song per individual in the analyses. However, for individuals that had a repertoire of two songs (less than 5%), we included one song of each type in our analyses (excluding these individuals from the analyses did not change the results). We digitized, analysed and measured each song using the Canary V1.24 software and used the following parameters in our analyses: for digitization, we used a sample rate of 22 050 Hz; for spectrogram analysis, we used a filter bandwidth of 352.87 Hz and a frame length of 256 points (and approximately 75% of brightness and contrast); and for power spectrum analysis, we used a filter bandwidth of 88.22 Hz and a frame length of 1024 points. All spectrographic analyses were done using a hamming window.

We measured the following variables on each sonagram (Fig. 1): total duration of the song (SongDur), duration of the theme and the trill (ThemeDur and TrillDur, respectively), number of trill notes (NNotes), trill interval (TI = TrillDur/(NNotes – 1)), and maximum and minimum frequencies of the whole song, the theme and the trill (SongMax, SongMin, ThemeMax, ThemeMin, TrillMax and TrillMin, respectively). TrillDur was measured from the middle part of the first note of the trill to the middle part of the last note. In addition, the frequency with the highest amplitude was measured on the power



**Figure 1.** Spectrogram (a) and power spectrum (b) of a typical *Z. capensis* song showing the variables measured. For acronyms see [Methods](#).

spectrum of the song, theme and trill (SongEmF, ThemeEmF and TrillEmF, respectively).

To reduce the possibility of finding artificial differences between the 1987 and 2000 breeding seasons due to methodological or technical problems, we took the following precautions: (1) all recordings for each season were made and digitized using the same tape recorder, and both recorders were checked for speed stability using a 500-Hz tone available in Canary sample files; and (2) the same observer selected all song samples and measured the material using the same software (Canary v1.24) and following standard procedures, without information about the precise location of each individual in the study area.

## Statistical Analysis

We initially looked for differences in song structure by performing a principal component analysis (PCA) on the log-transformed variables and using their correlation matrix. This procedure reduced the measured song variables into a small number of mutually independent variables that accounted for most of the variation included in the original data set. We used varimax raw rotation (Kaiser 1958) to obtain a clearer pattern of factor loadings. This multivariate approach allowed us to study general differences in song structure that might involve several variables at a time and helped us to understand how these variables are associated.

In addition, we also performed a univariate analysis. The two main reasons for analysing variables individually are: (1) acoustic theory makes specific predictions regarding individual variables of song structure, and (2) some

of the individual variables (particularly TI) have been extensively used and their analysis facilitates the comparison of our results with those of previous studies. Because several variables did not meet assumptions of homoscedasticity, we used nonparametric Mann–Whitney *U* tests for comparisons between habitats (within a given season) and between seasons (within a given habitat). Because we made multiple comparisons between groups using 14 different variables, we decided to use a Bonferroni corrected alpha to keep the global type I error smaller than 5%.

All statistical analyses were performed using the Statistica/w 4.1 package and all tests were two-tailed.

## RESULTS

The principal component analysis extracted six factors having eigenvalues in excess of 1 (Table 1). Factor 1 varied negatively with TrillDur, SongDur and NNotes. Factor 2 varied positively with maximum frequencies (SongMax and ThemeMax). An increase in factor 3 reflected an increase in TrillMin and a decrease in TI. Factor 4 varied negatively with minimum frequencies (SongMin and ThemeMin) and factor 5 varied negatively with emphasized frequencies (SongEmF and ThemeEmF). Finally, an increase in factor 6 reflected an increase in ThemeDur. Although these six axes taken together accounted for more than 80% of the variance in the original data set, the amount of the variation explained by each of them was relatively low (<20% in all cases).

Songs from open and closed habitats tended to differ in factor 3 (Fig. 2a). The lower factor 3 scores of the songs

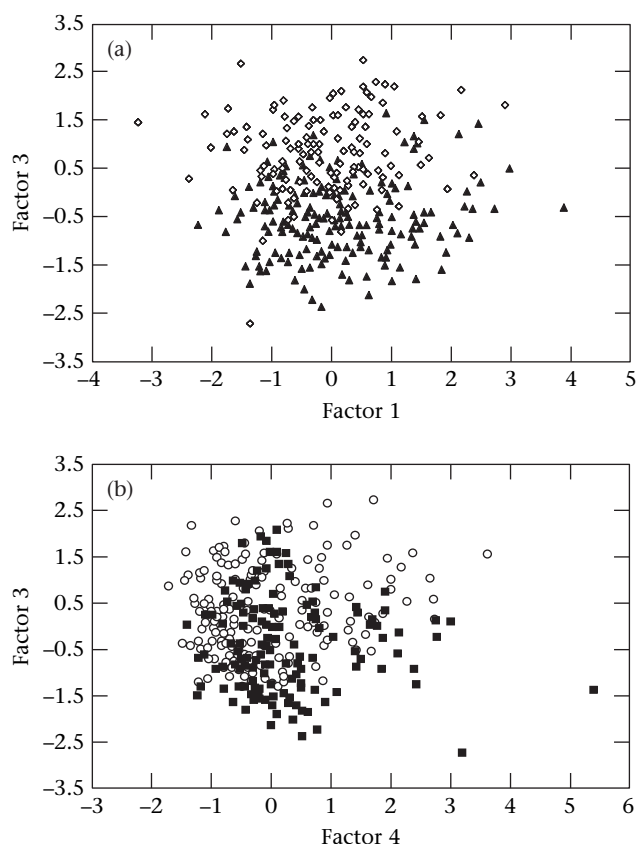
**Table 1.** Results of the principal component analysis performed on the log-transformed variables, using their correlation matrix

Variable*	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
SongEmF	0.13	-0.62	0.15	0.00	-0.89†	0.04
ThemeEmF	0.02	-0.01	0.05	-0.11	-0.89†	-0.12
TrillEmF	0.15	0.03	0.65	0.08	-0.12	0.02
SongDur	-0.78†	0.05	-0.14	0.02	0.09	0.58
ThemeDur	0.04	0.18	-0.02	0.02	0.03	0.95†
TrillDur	-0.96†	-0.05	-0.12	0.02	0.07	-0.09
SongMax	0.02	0.97†	0.05	0.02	0.03	0.08
SongMin	0.01	-0.01	0.13	-0.98†	-0.05	-0.01
ThemeMax	0.04	0.94†	0.07	-0.03	0.06	0.16
ThemeMin	0.01	0.01	-0.01	-0.97†	-0.03	-0.02
TrillMax	-0.32	0.52	-0.14	0.02	-0.25	-0.33
TrillMin	-0.03	0.01	0.74†	-0.23	-0.14	-0.04
NNotes	-0.90†	0.00	0.38	-0.10	0.02	-0.10
TI	0.11	0.09	-0.91†	0.06	0.07	0.04
Eigenvalues	2.50	2.13	2.04	1.98	1.72	1.40
% Variance	17.87	15.21	14.58	14.16	12.32	10.03

Varimax rotation was used to obtain a clearer pattern of factor loadings. The factors included are those with eigenvalues in excess of 1.

\*For acronyms see [Methods](#).

†Loadings in excess of 0.7.



**Figure 2.** (a) Scatterplot of factor 3 versus factor 1 obtained in the principal component analysis (PCA) for closed habitat songs ( $\blacktriangle$ ) and open habitat songs ( $\diamond$ ). Similar scatterplots were obtained when factor 3 was compared with the rest of the PCA factors. (b) Scatterplot of factor 3 versus factor 4 for the 1987 ( $\circ$ ) and 2000 ( $\blacksquare$ ) breeding seasons.

from closed habitats indicated that they had lower TrillMin and longer TI than those from the open habitats. The rest of the factors did not clearly separate the songs from the different habitats (data not shown). Songs from the two breeding seasons showed differences in factors 3 and 4 (Fig. 2b). Specifically, the 2000 sample was composed of songs with lower factor 3 and higher factor 4 scores, which indicates that these songs had lower minimum frequencies and higher trill intervals.

As mentioned above, we also performed a univariate analysis. Table 2 shows simple descriptive statistics for all the variables measured. The results of Mann–Whitney  $U$  tests of habitat and season differences in song structure are given in Tables 3 and 4, respectively. We found significant differences in TrillEmF, TrillMin, NNotes and TI between open and closed habitats irrespective of the season considered. In particular, closed habitat songs had lower frequencies and longer trill intervals than open habitat songs. As depicted in Fig. 3, the pattern of variation of TI was clinal rather than discontinuous. This pattern of variation was conserved between 1987 and 2000, showing a stability of at least 13 years. However, Mann–Whitney  $U$  tests between years showed significant differences in both theme and trill variables. Specifically, the songs from the 2000 season had lower frequencies (SongMin and TrillMin), longer ThemeDur and longer TI than the songs from 1987, irrespective of the habitat considered. In addition, some variables differed significantly between years only in one of the habitats: closed habitat songs from 2000 had longer SongDur and lower ThemeMin than the songs from 1987, and open habitat songs from 2000 had lower TrillMax and lower NNotes than those from 1987. To illustrate the differences between habitats and between breeding seasons, sonagrams of two songs from each habitat in each breeding season are shown in Fig. 4.

**Table 2.** Means  $\pm$  SD of songs according to breeding season and habitat

Variable*	1987 Season		2000 Season	
	Closed habitat N=137	Open habitat N=100	Closed habitat N=97	Open habitat N=56
SongDur	1538 $\pm$ 202	1576 $\pm$ 218	1650 $\pm$ 193	1615 $\pm$ 187
ThemeDur	939 $\pm$ 132	957 $\pm$ 151	1004 $\pm$ 145	1045 $\pm$ 129
TrillDur	491 $\pm$ 180	516 $\pm$ 178	530 $\pm$ 170	470 $\pm$ 161
SongEmF	4.52 $\pm$ 0.57	4.63 $\pm$ 0.49	4.48 $\pm$ 0.57	4.47 $\pm$ 0.45
ThemeEmF	4.73 $\pm$ 0.50	4.74 $\pm$ 0.59	4.56 $\pm$ 0.51	4.50 $\pm$ 0.39
TrillEmF	3.94 $\pm$ 0.51	4.47 $\pm$ 0.68	4.02 $\pm$ 0.76	4.42 $\pm$ 0.78
SongMax	7.79 $\pm$ 0.77	7.89 $\pm$ 0.77	7.64 $\pm$ 0.67	7.66 $\pm$ 0.83
SongMin	3.26 $\pm$ 0.28	3.28 $\pm$ 0.35	3.09 $\pm$ 0.30	3.14 $\pm$ 0.32
ThemeMax	7.66 $\pm$ 0.92	7.84 $\pm$ 0.85	7.50 $\pm$ 0.86	7.61 $\pm$ 0.91
ThemeMin	3.34 $\pm$ 0.33	3.32 $\pm$ 0.38	3.21 $\pm$ 0.36	3.20 $\pm$ 0.33
TrillMax	6.90 $\pm$ 0.37	6.90 $\pm$ 0.31	6.87 $\pm$ 0.40	6.66 $\pm$ 0.34
TrillMin	3.44 $\pm$ 0.15	3.64 $\pm$ 0.21	3.26 $\pm$ 0.15	3.45 $\pm$ 0.27
NNotes	6.78 $\pm$ 2.19	8.87 $\pm$ 3.16	6.02 $\pm$ 1.95	7.43 $\pm$ 2.19
TI	86 $\pm$ 12	67 $\pm$ 11	108 $\pm$ 17	73 $\pm$ 9

\*For acronyms see [Methods](#). Frequency and time variables measured in kHz and ms, respectively.

## DISCUSSION

We have shown the existence of persistent differences in the distribution of song characteristics between open and closed habitats at a microgeographical scale over a period of at least 13 years, with songs from the closed habitat (Talar) tending to have trills with longer trill intervals and lower frequencies than songs from the open habitats (marsh and steppe). However, the differences in song characteristics were not abrupt, and intermediate trill intervals and frequencies were found in the ecotone. Therefore, the observed pattern of variation could be described as clinal. The existence of these differences between habitats was suggested by the PCA and confirmed by the univariate analysis, and is consistent with the

results of previous studies of this species ([Handford 1981, 1988](#); [Lougheed et al. 1989](#); [Tubaro et al. 1993](#)) and with predictions from acoustic theory ([Morton 1975](#); [Wiley & Richards 1978](#); [Brown & Handford 1996, 2000](#)). Although longer trill intervals and lower frequencies are associated with closed environments, this does not necessarily mean that both variables are independent. For example, if shorter trill intervals are better suited for long-range communication in open habitats, performance constraints (such as limits on vocal tract movements, [Podos 1997](#)) might limit the frequency modulation of trill notes. In fact, [Handford & Lougheed \(1991\)](#) found that frequency bandwidth is usually narrower in dialects with shorter trill intervals in this species, and [Podos \(1997\)](#) argued that this finding is consistent with performance constraints found

**Table 3.** Results of Mann–Whitney *U* tests comparing songs from closed and open habitats within each season

Variable*	1987 Season Closed versus open habitat			2000 Season Closed versus open habitat		
	<i>U</i>	<i>Z</i> <sub>adj</sub>	<i>P</i>	<i>U</i>	<i>Z</i> <sub>adj</sub>	<i>P</i>
SongDur	6516	-0.64	0.52	2375	-1.29	0.20
ThemeDur	6319	-1.02	0.31	2218	-1.89	0.06
TrillDur	6378	-0.91	0.36	2101	-2.33	0.02
SongEmF	5938	-1.75	0.08	2698	-0.07	0.94
ThemeEmF	6798	-0.10	0.92	2597	-0.45	0.65
TrillEmF	3030	-7.33	<0.01†	1614	-4.17	<0.01†
SongMax	6343	-0.97	0.33	2699	-0.06	0.95
SongMin	6111	-1.42	0.16	2239	-1.81	0.07
ThemeMax	6165	-1.32	0.19	2576	-0.53	0.60
ThemeMin	6823	-0.05	0.96	2566	-0.57	0.57
TrillMax	6564	-0.55	0.58	1917	-3.03	<0.01†
TrillMin	2645	-8.10	<0.01†	1040	-6.38	<0.01†
NNotes	4032	-5.45	<0.01†	1660	-4.05	<0.01†
TI	1704	-9.87	<0.01†	136	-9.77	<0.01†

\*For acronyms see [Methods](#).

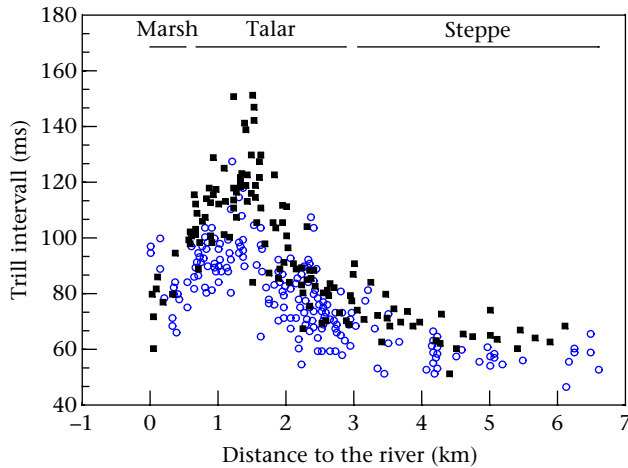
†Significant results after Bonferroni correction.

**Table 4.** Results of Mann–Whitney *U* tests comparing songs from the 1987 and 2000 breeding seasons, within each habitat type

Variable*	Closed habitat 1987 versus 2000			Open habitat 1987 versus 2000		
	<i>U</i>	<i>Z</i> <sub>adj</sub>	<i>P</i>	<i>U</i>	<i>Z</i> <sub>adj</sub>	<i>P</i>
SongDur	4532	-4.13	<0.01†	2429	-1.37	0.17
ThemeDur	4766	-3.68	<0.01†	1806	-3.67	<0.01†
TrillDur	5753	-1.75	0.08	2308	-1.82	0.07
SongEmF	6314	-0.65	0.52	2249	-2.04	0.04
ThemeEmF	5270	-2.69	0.01	2095	-2.60	0.01
TrillEmF	5373	-2.49	0.01	2427	-1.38	0.17
SongMax	6000	-1.26	0.21	2389	-1.52	0.13
SongMin	4138	-4.93	<0.01†	1955	-3.13	<0.01†
ThemeMax	6080	-1.11	0.27	2434	-1.35	0.18
ThemeMin	4942	-3.34	<0.01†	2050	-2.77	0.01
TrillMax	6312	-0.65	0.51	1702	-4.06	<0.01†
TrillMin	2456	-8.25	<0.01†	1361	-5.34	<0.01†
NNotes	5284	-2.70	0.01	1975	-3.07	<0.01†
TI	1876	-9.35	<0.01†	1727	-3.96	<0.01†

\*For acronyms see [Methods](#).

†Significant results after Bonferroni correction.

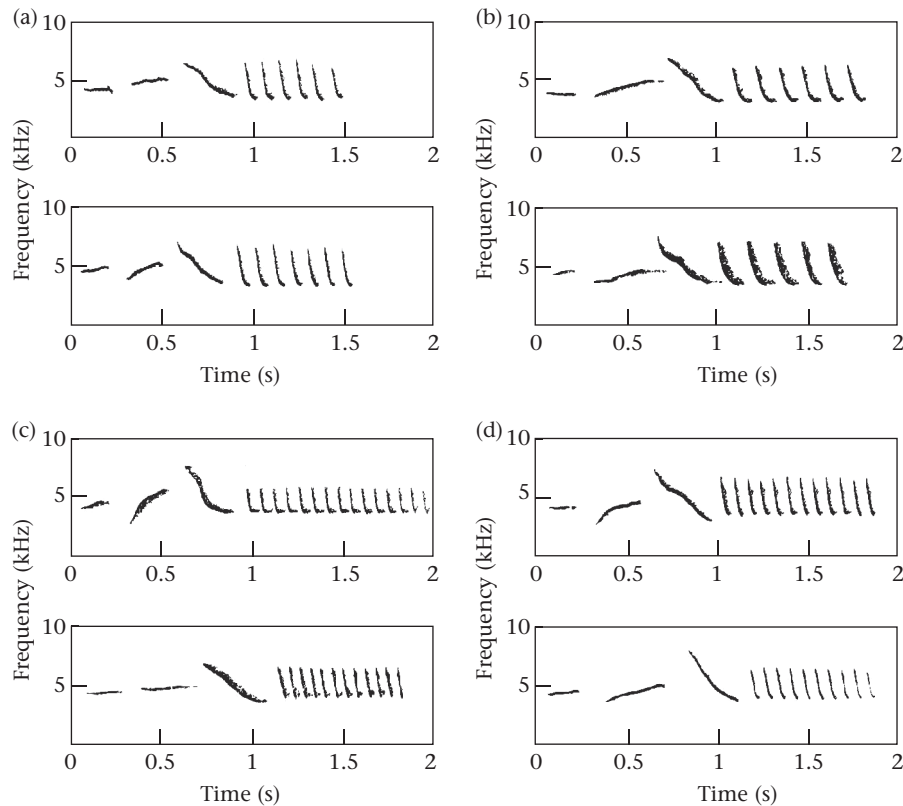


**Figure 3.** Scatterplot of trill intervals versus distance to the river for the 1987 (○) and 2000 (■) breeding seasons.

in other emberizids. Similarly, if trill duration was fixed (for example if the maximum duration of the trill was determined by the respiratory physiology), the number of notes and the trill interval would not be independent. The differences found between closed and open habitats in these variables were consistent with this kind of constraint

(TrillDur remained relatively constant in both kinds of habitats, but TI was significantly longer and NNNotes was significantly lower in the closed habitat than in the open habitats; see Table 3). Under this possible constraint, if longer trill intervals facilitate long-range communication in closed habitats, the number of notes must diminish if trill duration is to remain constant.

Because we found a persistent clinal pattern of song variation, we should address the problem of how this cline was formed and how it is maintained. The song in this species is learned (Egli 1971; Tubaro et al. 1997), and therefore, the maintenance of the cline (and of rufous-collared sparrow dialects in general) should result from juveniles copying the song type of their neighbours when they settle, as was shown to be the case in the white-crowned sparrow, *Zonotrichia leucophrys* (Nelson & Marler 1994; Nelson 2000). Moreover, song learning could not only explain the maintenance of the cline, but also its formation if juvenile males copy only the most clearly heard conspecific song models, because the songs or structures less effective for long-range communication would be the ones filtered by the environment (Hansen 1979; Nottebohm 1985). A study by Morton et al. (1986) of the Carolina wren, *Thryothorus ludovicianus*, suggested another possible mechanism for the formation of dialects: in this species, when juveniles hear unmodified songs as



**Figure 4.** Sonagrams illustrating the characteristics of rufous-collared sparrow songs from each habitat during each breeding season: (a) closed habitat in 1987, (b) closed habitat in 2000, (c) open habitat in 1987, (d) open habitat in 2000. Note that songs in closed habitats (a, b) had fewer notes and longer TI than those in open habitats (c, d). In addition, songs in closed habitats in 2000 (b) had longer TI, SongDur and ThemeDur than those in 1987 (a). Similarly, songs in open habitats in 2000 (d) had fewer notes, longer TI and longer ThemeDur than those in 1987 (c).

well as songs artificially modified by passage through the environment, they preferentially incorporate the former into their repertoires.

Previous studies of rufous-collared sparrows showed contrasting results regarding the stability of dialect features and boundaries. Handford (1981, 1988) found that dialect transitions between life zones in northwestern Argentina have been stable for at least 20 years, and a much longer stability (ca. 200 years) was inferred based on the higher fit of dialect distribution with the original habitat distribution than with the present one (Handford 1988; Handford & Lougheed 1991). In contrast, Tubaro et al. (1993) concluded that the Talar dialect disappeared from Punta Indio because of the destruction of native Talar habitat at that location 50 years earlier (the absence of previous song recordings, however, precluded the confirmation of this change). This diversity of results might be explained by the different geographical scales of these studies; when a habitat that occupies a small area disappears, the dialect used by individuals previously inhabiting the area may get overwhelmed by immigration of individuals from more extensive surrounding habitats, whereas changes at a regional scale could require much more time to occur (Tubaro et al. 1993). The studies mentioned have mainly analysed the association between dialects and habitat structure and the stability of the distribution of dialects over time, but ours is the first study to assess the structural temporal stability of particular dialects. In Estancia El Destino, although the location and general shape of the cline has remained stable for at least 13 years (and probably longer, see Tubaro et al. 1993), we detected several changes between 1987 and 2000, representing the first direct evidence of song change in this species. The PCA suggested that the songs from 2000 had lower minimum frequencies and longer trill intervals than those from 1987 and this was confirmed by the univariate analysis, which showed that the songs recorded during 2000 had longer trill intervals and lower minimum frequencies of the whole song and the trill than those recorded during 1987. These changes, however, did not affect the dialect boundaries, because they were not a consequence of a shift of the cline but of a change in the cline as a whole (see Fig. 3).

To ensure that any observed changes in the cline were real and not a consequence of methodological or technical problems such as differences in the criterion for choosing and/or measuring songs, changes in the speed of the tape recorder, or stretching of the recording tape, we took several precautions (see Methods) to avoid these problems. Moreover, various results suggest that the differences we observed were real. (1) Changes not only affected continuous variables (e.g. SongDur, TrillMin, etc.) but also the discrete one (NNotes), which cannot be altered by equipment malfunctioning. (2) Not all continuous variables changed in a systematic way between seasons. For example, although both the minimum frequency of the whole song (SongMin) and the trill (TrillMin) were significantly lower in 2000 than in 1987, six other frequency variables (SongEmF, ThemeEmF, TrillEmF, SongMax, ThemeMax and TrillMax) did not differ between seasons. Similarly, although song and theme duration

were shorter in 2000 than in 1987, trill duration remained unchanged. (3) Spectrographic analyses of the song backgrounds (particularly those containing stereotyped frequency tones, such as those of picazuro pigeons, *Columba picazuro*) showed no change in acoustic frequencies between breeding seasons.

In the closely related white-crowned sparrow, dialects have been shown to be stable for periods of 10–25 years (Baptista 1975; Trainer 1983; Chilton & Lein 1996). These studies also detected changes in some dialect frontiers as well as the extinction of some rare dialects. However, dialects of the white-crowned sparrow are defined differently from those of the rufous-collared sparrows, because in the former, dialects are based on qualitative characteristics of song structure (i.e. distinctive note structures) and in the latter, dialects are based on quantitative characteristics of song structure (i.e. temporal or frequency characteristics). Furthermore, the distribution of white-crowned sparrow dialects does not appear to coincide with changes in habitat, but instead appears to be a consequence of population changes such as local extinctions and colonization of empty patches of habitat (Baker 1975). Thus, song variants in this species are considered ‘neutral’ in terms of possible advantages for long-range communication.

Rufous-collared sparrow dialects, in contrast, are associated with habitat distribution and structure over extensive geographical space in a way that largely conforms to expectations from acoustical theory, suggesting an adaptive design for optimal long-range communication (Brown & Handford 1996, 2000). Thus, changes in dialect structure are only expected to occur after modification of the prevailing acoustical conditions of the environment. In this case, the longer trill interval and lower frequencies found in 2000 would be expected if all the habitats studied were more closed than in 1987 (note that the differences in the structure of songs between seasons were similar to the differences in structure between closed and open habitats in each season). Nevertheless, we did not detect any obvious change in habitat distribution or characteristics between breeding seasons. It must be borne in mind, however, that our study was not designed to measure vegetation variables, and therefore, we cannot rule out the existence of subtle changes in the characteristics of the habitats. Given that the amount of change needed to generate modifications in the structure of dialects is unknown, it is not possible to determine whether the subtle changes that might have occurred could be responsible for the observed change.

Climate could also affect avian vocalizations because sound velocity depends on air temperature, and the relative attenuation of different frequencies of the signal is influenced by air humidity (Nottebohm 1975). However, the statistics from the Servicio Meteorológico Nacional of Argentina did not show differences in temperature or humidity in the study area between 1987 and 2000. Unfortunately, information on other climatic variables that might be important in driving song structure (e.g. wind, Tubaro & Segura 1994) was not available.

The change observed in the cline might also be a consequence of habitat modifications that occurred in the past, probably long before 1987. This would imply the

existence of a delay in the adaptation of dialects to changes in the acoustical characteristics of the environment, which would be consistent with previous findings of dialects correlating with original, rather than present, vegetation in northwestern Argentina (Handford 1988; Handford & Loughheed 1991). This delay could be related to the high density of individuals of this species present in the study area, which could complicate the rapid selection of new song variants (even if they are better adapted to the environment). There are at least two reasons why a high density of individuals could have this effect. (1) Individuals are close to each other in a dense population, and therefore, songs travel short distances from a singer to its neighbours, consequently diminishing the selective pressure on the reduction of degradation. (2) During the learning process, individuals listen to songs from many adults in a dense population and a new song variant could therefore be 'diluted' because most of the singers will sing an 'old version' of the song.

The differences between seasons could also have been generated by demographic factors, such as migration. In theory, this could occur because of movements within the study area (individuals with longer trill intervals and lower frequencies moving from the woodland towards the ecotone and the open areas) or because of the arrival of individuals from outside the study area (probably from other closed habitats). If this were the case, however, changes in the variable means would be expected (because of the influence of a few migrants), but the kind of change observed, with most of the individuals from the 2000 season singing with longer trill intervals (see Fig. 3), would be difficult to explain. In addition, as can be seen in Fig. 3, trill intervals in the closed habitat were longer in 2000 than in 1987, and this can be explained neither by movements within the study area nor by the arrival of individuals from outside this area (because there were no dialects with longer trill intervals than those of the Talar dialect near the study area).

Finally, because the change in song structure was relatively small and the differences between dialects remained, the possibility of a neutral change should also be considered. In fact, the process of learning is not perfect, and learning errors can generate some degree of variation in song structure, which might be neutral in relation to the long-range communication properties of the song.

To discriminate between all of these possibilities and determine the ultimate causes of dialects' temporal change, the monitoring of song and habitat parameters should be a priority for future studies. One of the possible strategies could be to study areas that are suffering high degrees of transformation to assess how this affects song structure.

### Acknowledgments

We thank F. Gabelli for helping us to tape-record songs during the 1987 breeding season. We also thank the Elsa Shaw de Pearson Foundation for the permission and facilities for fieldwork. This work was supported by the

Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina.

### References

- Baker, M. C. 1975. Song dialects and genetic differences in white-crowned sparrows (*Zonotrichia leucophrys*). *Evolution*, **29**, 226–241.
- Baptista, L. F. 1975. Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). *University of California Publications in Zoology*, **105**, 1–52.
- Brown, T. J. & Handford, P. 1996. Acoustical signal amplitude patterns: a computer simulation investigation of the acoustic adaptation hypothesis. *Condor*, **98**, 608–623.
- Brown, T. J. & Handford, P. 2000. Sound design for vocalizations: quality in the woods, consistency in the fields. *Condor*, **102**, 81–92.
- Cabrera, A. L. 1949. Las comunidades vegetales de los alrededores de La Plata. *Lilloa*, **20**, 269–347.
- Cabrera, A. L. 1976. Regiones fitogeográficas Argentinas. In: *Enciclopedia Argentina de Agricultura y Jardinería*, Vol. 2. Sect. 1. Buenos Aires: Editorial Acme S.A.C.I.
- Chilton, G. & Lein, M. R. 1996. Long-term changes in songs and song dialect boundaries of puget sound white-crowned sparrows. *Condor*, **98**, 567–580.
- Egli, W. 1971. Investigaciones sobre el canto de *Zonotrichia capensis chilensis* (Meyen)(Aves, Passeriformes). *Boletín del Museo Nacional de Historia Natural de Chile*, **32**, 173–190.
- Gish, S. L. & Morton, E. S. 1981. Structural adaptations to local habitat acoustics in carolina wren songs. *Zeitschrift für Tierpsychologie*, **56**, 74–84.
- Handford, P. 1980. Return rates among highland rufous-collared sparrows. *Journal of Field Ornithology*, **51**, 176–177.
- Handford, P. 1981. Vegetational correlates of variation in the song of *Zonotrichia capensis*. *Behavioral Ecology and Sociobiology*, **8**, 203–206.
- Handford, P. 1988. Trill rate dialects in the rufous-collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Canadian Journal of Zoology*, **66**, 2658–2670.
- Handford, P. & Loughheed, S. 1991. Variation in duration and frequency characters in the song of the rufous-collared sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. *Condor*, **93**, 644–658.
- Handford, P. & Nottebohm, F. 1976. Allozymic and morphological variation in population samples of rufous-collared sparrow, *Zonotrichia capensis*, in relation to vocal dialects. *Evolution*, **30**, 802–817.
- Hansen, P. 1979. Vocal learning: its role in adapting sound structures to long-range propagation, and a hypothesis on its evolution. *Animal Behaviour*, **27**, 1270–1271.
- Kaiser, H. F. 1958. The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, **23**, 187–200.
- King, J. R. 1972. Variation in the song of the rufous-collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Zeitschrift für Tierpsychologie*, **30**, 344–373.
- Loughheed, S. C., Loughheed, A. J., Rae, M. & Handford, P. 1989. Analysis of a dialect boundary in chaco vegetation in the rufous-collared sparrow. *Condor*, **91**, 1002–1005.
- Miller, A. H. & Miller, V. D. 1968. The behavioural ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia*, **10**, 83–154.
- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.



- Morton, E. S., Gish, S. L. & van der Voort, M.** 1986. On the learning of degraded and undegraded songs in the Carolina wren. *Animal Behaviour*, **34**, 815–820.
- Nelson, D. A.** 2000. Song overproduction, selective attrition and song dialects in the white-crowned sparrow. *Animal Behaviour*, **60**, 887–898.
- Nelson, D. A. & Marler, P.** 1994. Selection-based learning in bird song development. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 10498–10501.
- Nottebohm, F.** 1969. The song of the chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialects. *Condor*, **71**, 299–315.
- Nottebohm, F.** 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *American Naturalist*, **109**, 605–624.
- Nottebohm, F.** 1985. Sound transmission, signal salience, and song dialects. *Behavioral and Brain Sciences*, **8**, 112–113.
- Parodi, L. R.** 1940. La distribución geográfica de los talaros de la Provincia de Buenos Aires. *Darwiniana*, **4**, 33–56.
- Podos, J.** 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, **51**, 537–551.
- Richards, D. G. & Wiley, R. H.** 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist*, **115**, 381–399.
- Shy, E.** 1983. The relation of geographical variation in song to habitat characteristics and body size in North American tanagers (Thraupinae: Piranga). *Behavioral Ecology and Sociobiology*, **12**, 71–76.
- Trainer, J. M.** 1983. Changes in song dialect distributions and microgeographic variation in song of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). *Auk*, **100**, 568–582.
- Tubaro, P. L. & Segura, E. T.** 1994. Dialect differences in the song of *Zonotrichia capensis* in the southern pampas: a test of the Acoustic Adaptation Hypothesis. *Condor*, **96**, 1084–1088.
- Tubaro, P. L., Segura, E. T. & Handford, P.** 1993. Geographic variation in the song of the rufous-collared sparrow in eastern Argentina. *Condor*, **95**, 588–595.
- Tubaro, P. L., Handford, P. & Segura, E. T.** 1997. Song learning in the rufous-collared sparrow (*Zonotrichia capensis*). *Hornero*, **14**, 204–210.
- Wasserman, F. E.** 1979. The relationship between habitat and song in the white-throated sparrow. *Condor*, **81**, 424–426.
- Wiley, R. H.** 1991. Associations of song properties with habitat for territorial oscine birds of eastern North America. *American Naturalist*, **138**, 973–993.
- Wiley, R. H. & Richards, D. G.** 1978. Physical constraints on acoustic communication in the atmosphere. Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, **3**, 69–94.