

GEOGRAPHIC VARIATION IN THE SONG OF THE RUFIOUS-COLLARED SPARROW IN EASTERN ARGENTINA¹

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Abstract. Variation in trill features of Rufous-collared Sparrow (*Zonotrichia capensis*) song is described in three sites located on the northeast coast of Buenos Aires Province, Argentina. There is a distinctive "talar" dialect in sites supporting natural woodlands. This dialect is characterized by slower trills with lower minimum frequencies than the one present in the open grassy fields ("steppe" dialect). Talar dialect is absent in a site where natural woodlands have been replaced by grassy fields and open man-made parks, suggesting that the vocal tradition changed after habitat modification. Detailed analysis reveals that talar and steppe dialects intergrade in a song cline, following the vegetational ecotone. This song cline has been stable in location and features during the last decade, even though there were no geographic barriers impairing population or cultural exchange between habitats.

Key words: *Rufous-collared Sparrow; Zonotrichia capensis; trill variation; dialect; song cline.*

INTRODUCTION

Bird song dialects, that is, particular types of songs shared by birds inhabiting the same area, have been described in several species (see Munding 1982). Two of the most studied are the White-crowned Sparrow (*Zonotrichia leucophrys*) (see Baker and Cunningham 1985, Kroodsmas et al. 1985) and the Rufous-collared Sparrow or Chingolo (*Z. capensis*) (Nottebohm 1969, 1975; Nottebohm and Selander 1972; King 1972; Handford and Nottebohm 1976; Handford 1981, 1988; Handford and Loughheed 1991; Loughheed and Handford 1992).

The song of this species has two parts: an introduction and a final portion referred to as "theme" and "trill," respectively. The theme is usually composed of two to five whistled ascending or descending notes. According to the number, shape and ordering of the notes, it is possible to distinguish different themes. Within an area, each male usually sings an individually distinctive theme. On the other hand, the main pattern of trill variation is among populations. In particular, trill interval (time between consecutive notes in the trill) is relatively constant within an area, but it changes among life zones,

thus giving rise to regional dialects (Nottebohm 1969, 1975; Handford 1981, 1988; Loughheed et al. 1989). Rufous-collared Sparrow dialects have been well studied in northwestern Argentina where there is a strong pattern of habitat variation with longitude and altitude (King 1972; Nottebohm 1975; Handford and Nottebohm 1976; Handford 1981, 1988; Handford and Loughheed 1991). These studies have shown the existence of a relationship between trill dialect and vegetation, and a high temporal stability in regional dialect distribution during the last two decades.

In areas with homogeneous vegetation trill features seem to be relatively constant over great distances. For example, in the lowlands of Buenos Aires, Santa Fe and Córdoba Provinces, Nottebohm (1969, 1975) found a relatively homogeneous dialect (hereafter referred to as "steppe" dialect), characterized by a trill interval of about 60-70 msec. This area is also characterized by a homogeneous herbaceous steppe (the "Argentine pampas," Cabrera 1976).

Here, we describe the geographic pattern of trill variation of the Rufous-collared Sparrow over a small geographic area located near the northeast coast of the Buenos Aires Province, Argentina. The original habitats present in this area included marsh, open woodland locally termed "talar" for the dominant tree, "tala" (*Celtis tala*), and steppe. However, at certain sites within this

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area present-day vegetation differs from the original one, because human activities have replaced the talar by grassy fields, gardens and parks. This situation opens the possibility for making song comparisons among sites where the original vegetation still remains and those in which this vegetation has been replaced during the last few decades. In particular, the aim of this study is: (1) to provide new evidence about the association between dialects and vegetation, (2) to study the shape and temporal stability of the dialect boundaries, and (3) to assess the possible effect of habitat change upon dialect distribution.

MATERIALS AND METHODS

The study area was located in the Partido of Magdalena, on the northeast coast of Buenos Aires Province, Argentina (Fig. 1). From the Río de la Plata inland, three different habitats can be distinguished:

- (1) Marsh: a seasonally flooding lowland and higher ground with grass cover, near the coast of the Río de la Plata. There are three dominant communities of plants: *Salicornia ambigua-Paspalum vaginatum*; *Scirpus olmeri-Paspalum vaginatum-Distichlis* spp.; and *Mentha pulegium-Pamphalea bupleurifolia*.
- (2) Talar: a xeromorphic woodland comprising several tree species: *Celtis tala* (fam. Ulmaceae); *Scutia buxifolia* (fam. Rhamnaceae); *Jodina rhombifolia* (fam. Santalaceae) and *Acacia caven* (fam. Leguminosae), among others.
- (3) Steppe: an herbaceous open grassland, essentially without trees (with the exception of some planted rows of *Eucalyptus* sp., and a few isolated *C. tala*). The main herbaceous communities present in this area are: *Stipa charruana-Cynara cardunculus-Diodia dasycephal*a; *S. charruana-Danthonia montevidensis-Eryngium ebracteatum*; *Stipa papposa-Stenotaphrum secundatum-Distichlis* spp. Detailed descriptions of these communities can be found in Cabrera (1949), Parodi (1940), Vervoort (1967) and Leon et al. (1979).

Within this area, we studied three sites (Fig. 1):

Site A—Estancia El Destino: an area of about 7 km². Part of this area is a private reserve, where

all the natural habitats are in a relatively good state of conservation.

Site B—Punta Indio: an area with some tourist activity, where marked modifications in the original vegetation have been made, mainly through the elimination of the talar woodland and its replacement by grassy fields, gardens and open parks. The size of the sampled area was about 3 km², and comprises the marsh and steppe habitats as well as the place occupied in the past by a well developed talar.

Site C—Estancia Luis Chico: an area of about 1 km², including only the talar and the steppe habitat. This area has been partially altered because of the past exploitation of calcareous deposits, agricultural practices, and the introduction of cattle. In this site the talar exists as a secondary growth and its physical structure is different from that in Site A, mainly because of the small stature and the dispersed distribution of trees.

Song sample. The songs of 897 adult individuals were recorded using a UHER 4000 Report-L at a speed of 9.5 cm/sec, and a directional cardioid Lec 980 LEEA microphone. Wild *Z. capensis* singers are always males (King 1972), but the possibility that a small fraction of females sometimes sing cannot be ruled out. Eight hundred and forty-five individuals were recorded at Site A between October and January (59 in 1984–1985; 24 in 1985–1986; 149 in 1986–1987; 215 in 1987–1988; 72 in 1988–1989; 127 in 1989–1990; and 199 during October 1991); 25 at Site B during January (16 in 1988–1989; and 9 in 1989–1990); and 27 at Site C, on 13 January 1989.

On each sonogram (made with a Kay Electric Sonagraph 7029-A, with the wide band setting and filtered to pass the 80–8,000 Hz frequency range) five trill features were measured: total duration, number of notes (NN), trill interval (TI) (calculated as trill duration/[NN – 1]), maximum and minimum frequencies (FMAX and FMIN, respectively).

Statistical analysis. We made a two-way multivariate analysis of variance (MANOVA) using three variables (IT, FMAX and FMIN), and the SYSTAT statistical package (Wilkinson 1987). In this analysis we included the 1987–1988 song data from Site A, permitted by the completeness of this sample. We also included the data from Site C, and the pooled data of 1988–1989 and 1989–1990 from Site B. In this case, the possi-

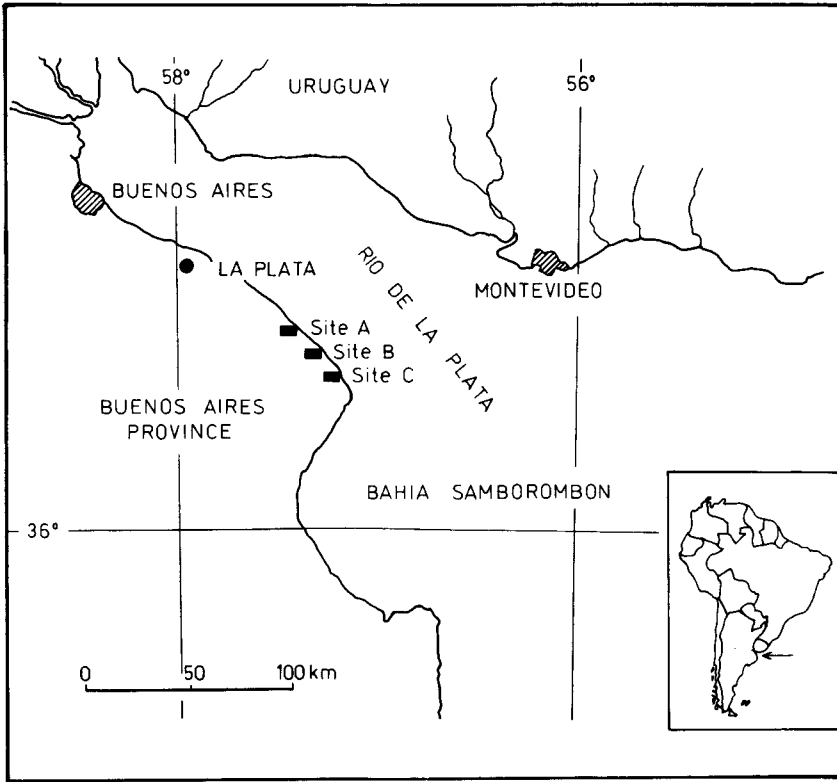


FIGURE 1. Map showing the location of the study area: Site A (Estancia El Destino); Site B (Punta Indio); and Site C (Estancia Luis Chico).

bility of recording the same bird twice was negligible for three reasons. First, the density of singers found at this site is high. Second, the song recordings were made in different neighborhoods for each period. Third, estimates of the disappearance rate for adult Rufous-collared Sparrows are high, ranging from 30 to 77.6% (Miller and Miller 1968, Handford 1980).

Because of the small number of birds recorded at marsh habitat in Sites A and B, we excluded these data from the formal analysis. However, they are plotted in Figures 2 and 3 for comparison.

RESULTS

Two-way MANOVA showed a significant effect of site (Wilks' Lambda = 0.607; $F_{6,496} = 23.40$; $P < 0.001$), habitat (Wilks' Lambda = 0.880; $F_{3,248} = 11.27$; $P < 0.001$), and site-habitat interaction (Wilks' Lambda = 0.791; $F_{6,496} = 10.28$; $P < 0.001$). Student *t*-test (Bonferroni-adjusted probabilities) showed that this interaction is due

to the fact that talar and steppe songs differed at Sites A and C, but not at Site B (Table 1).

For convenience, we introduce the term "talar dialect" to refer to the slower trilled songs (higher TI values) heard in talar, and use the term "steppe dialect" to refer to the faster TI songs heard on steppe (Figs. 2, 4). At Site A, talar dialect also showed a lower FMIN than the steppe dialect (Fig. 3). Although there are clear song differences in relation to the vegetation type, the pattern of song change is clinal and accompanied the environmental ecotone. Figure 2 shows that this TI cline at Site A has been stable during at least the last six years. Because of the small size and uneven spatial distribution of the song samples taken during 1984–1985 and 1985–1986, they are not presented, although they show essentially the same pattern of variation described above.

DISCUSSION

Our results show the existence of a tight relationship between trill features and vegetation

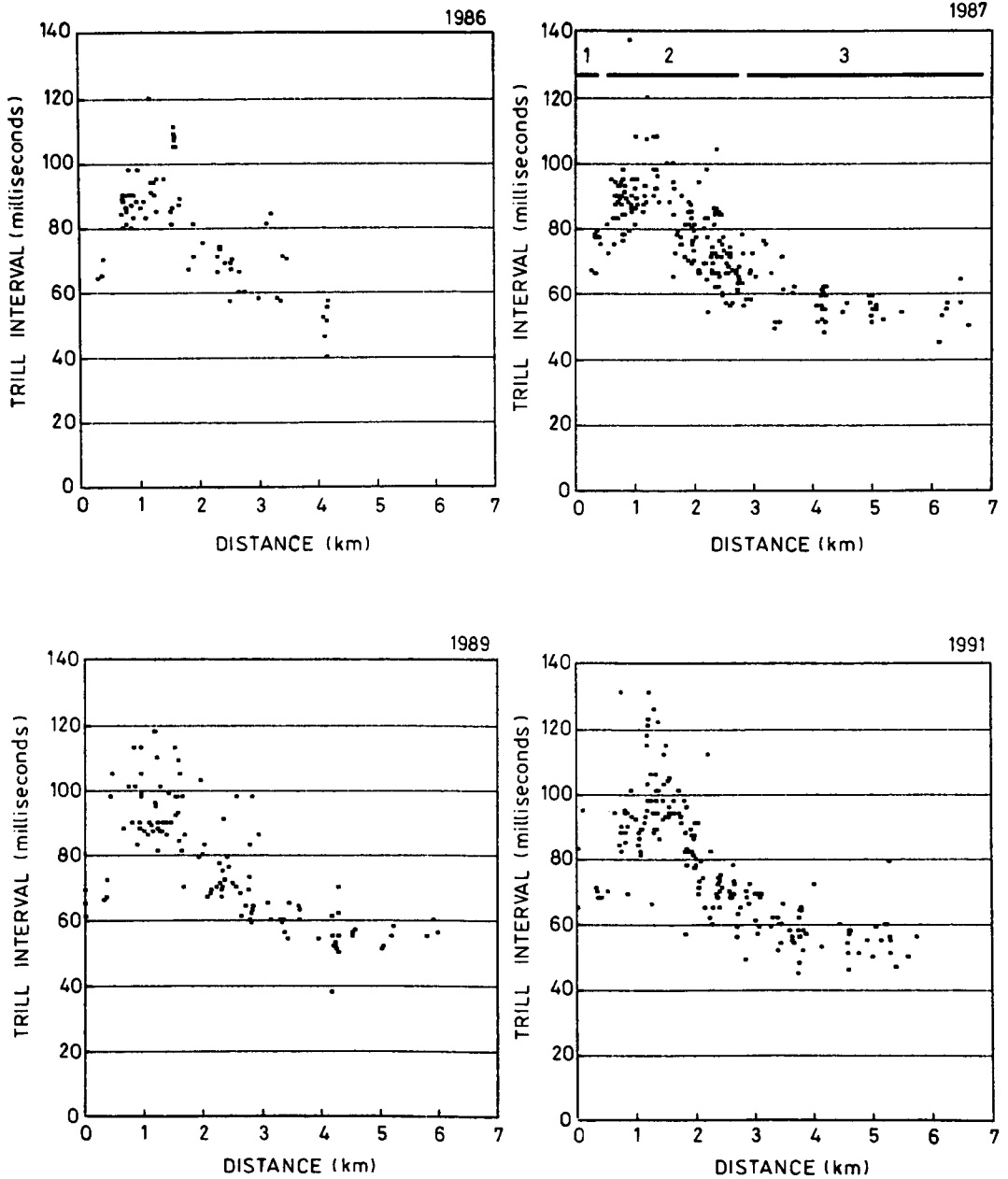


FIGURE 2. Individual trill interval values in Site A, from the coast of the Río de la Plata (marked as zero on the X axis) to the inland. The year in which the song sample was taken is indicated at top right of each graph. Along the top of the 1987 graph, the lines 1, 2, and 3 indicate the area occupied by marsh, talar and steppe habitats, respectively.

type, similar to those reported in other areas from Argentina. The songs found in talar woodland have longer TI and lower FMIN than those found on the steppe. This syndrome of song structure agrees with trends reported from other Argentine

areas, which showed faster trills (lower TI) in open scrub and grasslands than in more forested areas (Nottebohm 1975; Handford 1981, 1988). This trend is also compatible with current ideas on the acoustic properties of natural environ-

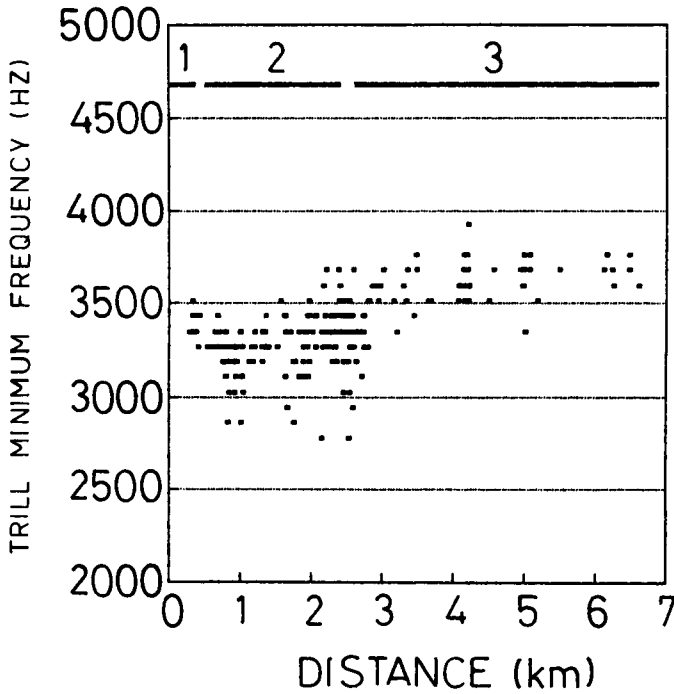


FIGURE 3. Diagram of the minimum frequency variation in Site A, during the season 1987–1988. Lines at the top of the graph indicate the approximate extent of each habitat type, as in Figure 2.

TABLE 1. Descriptive statistics of songs from Sites A, B, and C.

	Original habitat		Student's <i>t</i> test ^b	
	Talar <i>n</i> = 164	Steppe <i>n</i> = 43	<i>t</i> (205)	<i>P</i>
Site A (Ea. El Destino)				
Trill interval (milliseconds)	80 ± 13 ^a	57 ± 7	10.935	0.000*
Minimum frequency (kHz)	3.3 ± 0.2	3.6 ± 0.1	12.350	0.000*
Maximum frequency (kHz)	6.9 ± 0.3	6.8 ± 0.2	1.550	0.123
	Original habitat		Student's <i>t</i> test ^b	
	Talar <i>n</i> = 13	Steppe <i>n</i> = 9	<i>t</i> (20)	<i>P</i>
Site B (Punta Indio)				
Trill interval (milliseconds)	61 ± 4	62 ± 6	0.591	0.561
Minimum frequency (kHz)	3.6 ± 0.2	3.6 ± 0.3	0.149	0.883
Maximum frequency (kHz)	6.9 ± 0.4	7.4 ± 0.5	2.742	0.013
	Original habitat		Student's <i>t</i> test	
	Talar <i>n</i> = 16	Steppe <i>n</i> = 11	<i>t</i> (25)	<i>P</i>
Site C (Ea. Luis Chico)				
Trill interval (milliseconds)	69 ± 8	61 ± 5	3.425	0.002*
Minimum frequency (kHz)	3.6 ± 0.1	3.6 ± 0.1	0.918	0.367
Maximum frequency (kHz)	7.4 ± 0.4	7.6 ± 0.4	1.008	0.323

^a $\bar{x} \pm SD$.

^b Two tailed.

^c These *P*-values are not adjusted for multiple comparisons. We assume that there are nine multiple comparisons to be adjusted. Those comparisons with a Bonferroni-adjusted *P*-value of <0.05 are indicated with an asterisk.

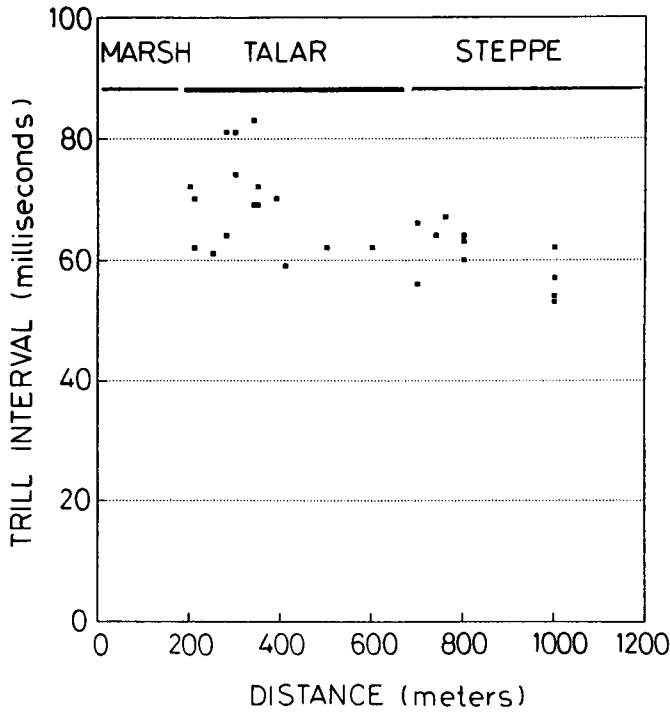


FIGURE 4. Diagram of the trill interval variation in Site C, during the season 1988–1989.

ments: slow modulated signals are favored in forests, because they avoid the acoustic degradation generated by the accumulation of echos. In open fields, the main source of acoustic degradation is random amplitude fluctuation produced by nonstationary heterogeneities. This favors signals with high rates of repetition (Wiley and Richards 1978, Richards and Wiley 1980).

At Site A, the transition from 60 msec TI in steppe to 100–120 msec TI in talar woodland occupies only 2 km, in an area where there are no physical barriers to population or cultural exchange between dialectal populations. Several stepped song transitions have been reported in northwestern Argentina associated with strong environmental gradients (Nottebohm 1975, Handford and Nottebohm 1976, Handford 1988, Loughheed et al. 1989), pointing out again the importance of habitat features, particularly the vegetation type, in the process of dialect differentiation.

Talar habitat occupies, even in the undisturbed Site A, only a small area, but that seems sufficient to affect the cultural evolution of Rufous-collared Sparrow song. Recordings from

1984–1985 to 1991 show the temporal stability of the TI cline and, from songs recorded and heard in the talar in 1978, it is possible to back-track the existence of the “talar” dialect for at least 14 years. This result at a local scale also agrees with evidence of regional dialect stability in northwestern Argentina, obtained during the last 20 years (Nottebohm and Selander 1972; Nottebohm 1975; Handford and Nottebohm 1976; Handford 1981, 1988).

The presence of a differentiated trill dialect in Sites A and C, where natural vegetation has been relatively preserved, contrasts with the absence of the talar dialect at Site B, an area where historical information indicates the existence of well developed talar woodland during the first half of this century (Parodi 1940). These facts suggest that the talar dialect could have gone extinct in Site B after the habitat changed. This scenario differs with that developed by Handford (1988), about the persistence of original song dialects in northwestern Argentine areas, where natural vegetation has been drastically modified by human activities. However, these apparent contradictory scenarios may be the result of the different

geographic scales in which trill variation was studied. The area occupied by dialects analyzed by Handford (1988) was at least ten times larger than that reported here for talar dialect. Because of the small area occupied by talar dialect and its great perimeter of contact with steppe dialect, it is possible that immigration movements of birds from surrounding open areas is responsible for the rapid talar dialect disappearance at Site B.

Song replacement could occur not only as a result of a demographic process, but also as a selective learning phenomenon, as proposed by the "Ranging hypothesis" (Morton 1986) and the "Acoustic adaptation hypothesis" (see Rothstein and Fleischer 1987). Accordingly, the song tradition that is better adapted to propagate at distance in the environment would be preferentially copied by birds (Hansen 1979, Gish and Morton 1981, Nottebohm 1985, Morton 1986, Morton et al. 1986). This process could shift the dialect frontier after the habitat changed, expanding steppe dialect over talar altered areas. Again, this dialect replacement could be very rapid (about a decade) at Site B because of the great frontier with steppe dialect and the small size of talar dialect population. If this interpretation is correct, changes in a regional scale could require hundreds or thousands of years.

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