SHORT COMMUNICATIONS

DIALECT DIFFERENCES IN THE SONG OF
ZONOTRICHIA CAPENSIS IN THE SOUTHERN PAMPAS:
A TEST OF THE ACOUSTIC ADAPTATION HYPOTHESIS[1]

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Although geographic variation in song is a relatively common phenomenon in songbirds (see Mundinger 1982), there are only a few cases in which the physical properties of song have been related to habitat structure. For example, studies of the White-throated Sparrow (*Zonotrichia albicollis,* Wasserman 1979, Waas 1988), the Summer Tanager (*Piranga rubra,* Shy 1983), the Northern Cardinal (*Cardinalis cardinalis,* Anderson and Conner 1985), and the Great Tit (*Parus major,* Hunter and Krebs 1979) indicate the use of lower frequencies and narrower bandwidth in forested than in more open habitats. The Rufous-collared Sparrow (*Zonotrichia capensis*) is unique in this regard because it shows higher frequency and broader bandwidth associated with more closed and mesic environments (Nottebohm 1975, Handford and Lougheed 1991). In addition, it has a complex system of dialects which are clearly distributed following vegetation structure (Nottebohm 1969, 1975; Handford andNottebohm 1976; Handford 1981, 1988; Lougheed et al. 1989; Handford and Lougheed 1991; Tubaro et al. 1993). In this species, dialects are defined according to the rate of note delivery in the final (trilled) part of the song. This "trill interval" is usually longer in closed (forested) areas than in open ones (for apparent exceptions in Handford 1988).

At a community level of analysis, several studies have reported song differences between habitats. Chappuis (1971) and Morton (1975) found that the frequencies used by tropical forest birds were lower than those used by species living in open tropical habitats. In addition, birds living in open and edge habitats usually employ broad band and rapidly modulated sounds in relation to those from closed forested areas (Morton 1975, Wiley 1991).

Different hypotheses have been proposed to account for these patterns of variation. Marler (1952) suggested that the song of a local population of a species must differ significantly from that of other species sharing the same local habitat. Nottebohm (1969) suggested that populations adapted to different habitats will evolve markers as a reproductive isolation mechanism. In this case, dialect markers are arbitrary and not correlated with habitat structure. This hypothesis does not predict the observed convergence in song features among disjunct areas supporting similar habitats (Handford 1988).

Finally, it has been proposed that variation in song structure may represent adaptations for long range communication (see for examples: Morton 1975, Nottebohm 1975, Marten and Marler 1977, Marten et al. 1977, Nottebohm 1985, Ryan and Brenowitz 1985, Handford 1988, Wiley 1991). According to this Acoustic Adaptation Hypothesis or AAH (Rothstein and Fleischer 1987) and the current ideas about habitat acoustics, slowly 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 low rate amplitude fluctuation produced by moving cells of air with different temperature and humidity. This favors signals with high rates of repetition (Wiley and Richards 1978, Richards and Wiley 1980). Here, we report the existence of a cline in song structure which partially contradicts naive predictions derived from the AAH.

METHODS

The study area is located in the Villarino region, Buenos Aires Province, Argentina, along the road from Médanos (38°50′S, 62°42′W) to Balneario Chapalcó (38°38′S, 63°05′W). This area is 70 km west to the Atlantic coast and the Bahia Blanca city. The vegetation comprises a transition from a grassland (Pampean Province, Southern Pampean district) to a short-statured xeromorphic woodland (Espinal Province, Calden district, Cabrera and Willink 1980). The grassland is an open herbaceous steppe with abundance of *Stipa* and *Piptochaetium* species. The woodland is a dense and complex assembly of leguminous trees dominated by the "calden" (*Prosopis caldenia*) and shrubs like *Hyalis argentea, Suadea divaricata, Allenrolfea pata-*
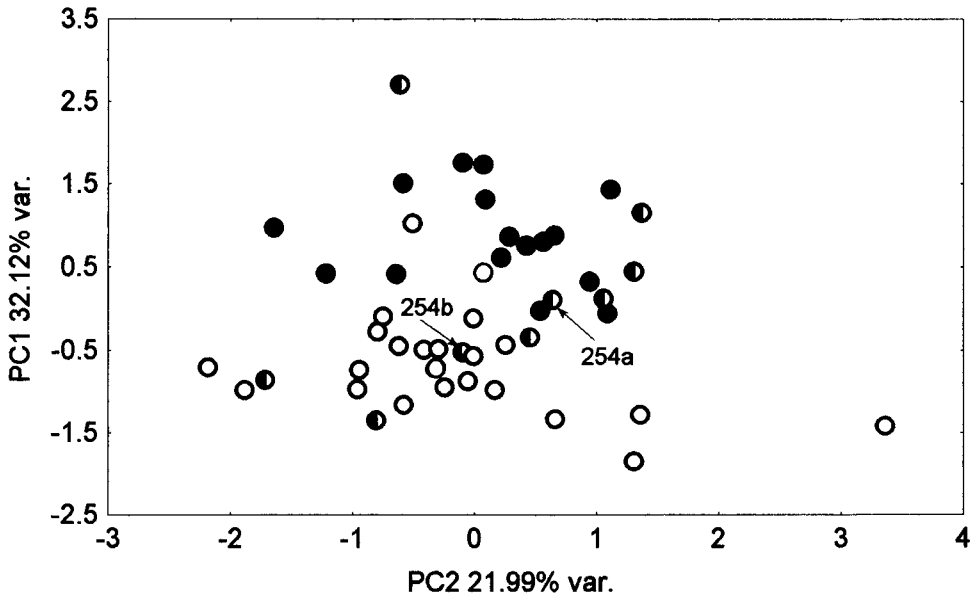

FIGURE 1. Scatterplot of PC1 vs. PC2 scores from the analysis excluding TRINT. PC1 corresponds to an axis of decreasing TRBAND and TRLEN, and increasing TRMIN. PC2 corresponds to an axis of decreasing THBAND. Songs from the woodland and the grassland are indicated with closed and open circles, respectively. Half painted circles represent individuals living in the ecotone between these two habitats. Songs 254a and b belong to a single individual having a repertoire of two song types. For acronyms see METHODS.

gonica, Heterostachys olivacens and *Cyclolepis genistoides*. Many of these species are adapted to the sandy and halophilous soil, and an arid climate (rainfall about 400–500 mm).

During 15 and 16 November 1993, we recorded the songs of 47 adults using a Uher 4000 Report-L and a Lec 970 microphone (manufactured by Leea). Since the song of the Rufous-collared Sparrow is generally highly stereotyped (Nottebohm 1969), we made a sonogram of the best recorded song of each individual (except in a case where the subject had a repertoire of two song types). On each sonogram (made with a Proaudio Spectrum 16 Sound Blaster [Media Vision] and the ADDA 16 software [LIS 1992]) we measured the following variables (see Handford and Lougheed 1991): Maximum and minimum frequencies and duration of both the introductory part of the song or "theme" and trill (THMAX, THMIN, THLEN, TRMAX, TRMIN, TRLEN); theme and trill bandwidth (THBAND and TRBAND); and song length (SOLEN). Mean trill interval (TRINT) was calculated as TRLEN/(number of trill notes − 1). TRLEN was measured from the middle point of the first trill note to the midpoint of the last one (Table 1).

We looked for differences in song structure performing a principal component analysis (PCA) on the log transformed variables and using their correlation matrix. This procedure reduced the variables measured on songs to a small number of mutually independent variables which account for most of the variation included in the original set of data. Since TRINT varies with habitat we excluded this variable from the PCA.

The aim of this procedure was to avoid the possibility that the results were driven mainly by TRINT, and to facilitate comparisons with the previous work of Handford and Lougheed (1991). Then, we performed a multivariate analysis of variance (MANOVA) using the principal component scores as the dependent variables, and the habitat type as the independent (grouping) one. Finally, we made a canonical variates (discriminant) analysis using the original variables for describing song differences between habitats. All statistical tests were performed using the STATISTICA/w 4.1 package.

RESULTS

The principal component analysis (excluding TRINT) showed that PC1 varies inversely with both TRLEN and TRBAND, and positively with TRMIN. PC2 corresponds to an axis of decreasing THBAND, and PC3 is not readily interpretable (Table 2). Taken together, these three axes account for 73.50% of the total variance in the original set of data.

Songs from grassland areas have longer trills with lower minimum trill frequencies and broader trill bandwidth than those from woodland areas (Fig. 1). There is a negative correlation between PC1 scores and TRINT (Fig. 2; $P \ll 0.001$; $R^2 = 0.425$) indicating that the longer the TRINT, the higher both the TRBAND and the TRLEN, and the lower the TRMIN. Song differences between habitats were confirmed by the MANOVA showing a significant effect of the habitat on song structure (Wilks' Lambda = 0.514; $F_{3,44} = 13.871$; $P < 0.00001$). Stepwise discriminant analysis
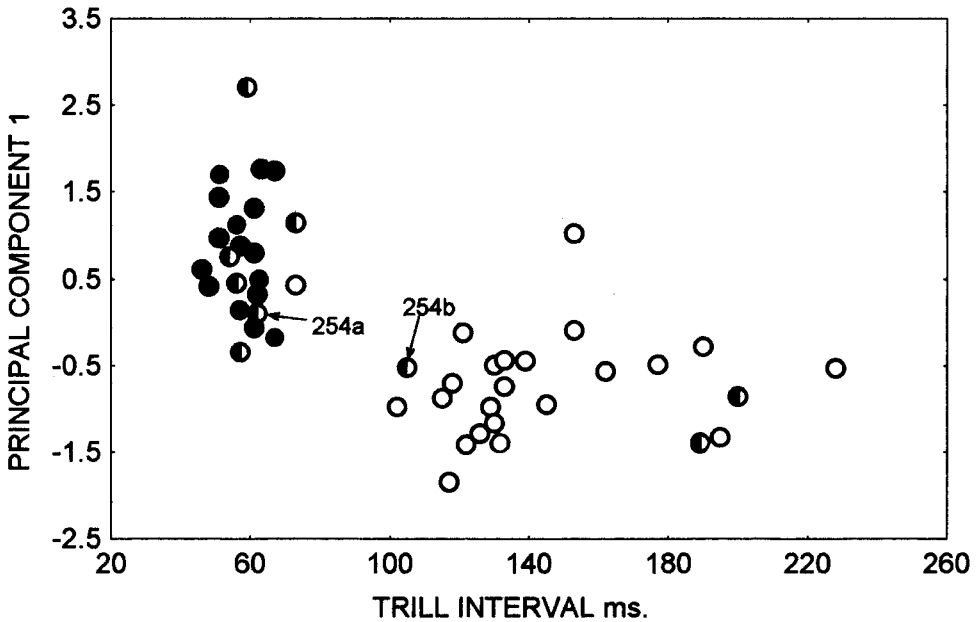
FIGURE 2.   Scatterplot of PC1 scores vs. TRINT. References as in Figure 1. For acronyms see METHODS.

based on the original data set (10 song variables by 48 songs matrix) indicated that open sites have significantly longer TRINT, broader TRBAND, and lower TRMIN than the songs from closed habitat (see Table 1). Differences between groups are striking, with 88% (22/25) of correct classification for songs from the woodland versus 87% (20/23) for songs from the grassland.

DISCUSSION

This study supports earlier reports of a relationship between song structure and habitat. In particular, songs from the open grassland have longer TRINT, broader TRBAND and lower TRMIN than those from closed woodland vegetation. There is a narrow zone of juxtaposition between these two dialects (about 1 km wide) which coincides with the ecotone between the closed

woodland and the open grassland. Inside this area birds sing either the woodland dialect or the grassland one, rather than intermediate songs. This is particularly evident for bird 254, which has a repertoire of two song types. Each type conforms to one of the two dialects present in this area (see Fig. 1 and Fig. 2).

Particularly interesting is that songs from the open (grassland) habitat have longer TRINT, contrasting to the commonly observed trend in other areas from Argentina (Nottebohm 1969, 1975; Handford 1981, 1988; Tubaro et al. 1993). This finding also differs from the AAH prediction about the occurrence of longer TRINT in forested areas as a way of reducing signal degradation produced by the accumulation of echos. However, these songs are "normal" (i.e., conforming AAH predictions) regarding the use of wider bandwidth in open areas (Chappuis 1971, Morton 1975, Wiley 1991), but con-

TABLE 1.   Descriptive statistics of songs from closed and open habitats. Frequency and temporal variables are expressed in Hertz and in milliseconds, respectively. For acronyms see METHODS.

	THMAX	THMIN	THBAND	TRMAX	TRMIN	TRBAND	THLEN	TRLEN	SOLEN	TRINT
Woodland ($n = 25$)										
Min.	5,533	1,883	2,502	4,901	2,340	1,081	645	200	1,025	46
Max.	7,236	3,359	4,054	6,926	3,913	4,224	1,320	970	2,000	200
Mean	6,123	3,041	3,082	6,067	3,520	2,547	984	488	1,569	71
SD	430	270	451	460	430	631	184	199	242	39
Grassland ($n = 23$)										
Min.	4,675	1,119	1,081	5,624	2,144	1,899	620	305	1,195	73
Max.	6,898	3,594	4,481	6,778	4,201	4,219	955	1,290	2,355	228
Mean	6,053	3,211	2,883	6,314	2,712	3,602	811	609	1,559	140
SD	535	485	631	300	448	531	96	232	274	33

TABLE 2. Factor loadings from the principal component analysis carried out on the log transformed song variables excluding TRINT. For acronyms see METHODS.

Component loadings	Component		
	PC1	PC2	PC3
THMAX	0.245	−0.534	−0.588
THMIN	0.040	0.401	0.205
THBAND	0.209	−0.722*	−0.623
TRMAX	−0.672	−0.173	−0.300
TRMIN	0.776*	0.241	−0.217
TRBAND	−0.930*	−0.226	−0.023
THLEN	0.492	0.530	−0.539
TRLEN	−0.712*	0.396	−0.359
SOLEN	−0.343	0.658	−0.642
Eigenvalues	2.891	1.979	1.745
% Variance	32.12	21.99	19.39

* Loadings greater than 0.7.

trast with the previous finding of Handford and Lougheed (1991) about the use of narrow bandwidth in the songs of the Rufous-collared Sparrow in open habitats from northwestern Argentina.

There are at least two important features of the grassland in the study area which can account for the variation in song structure. First, there is a very low density of singers in the grassland compared to the woodland, and previous works have suggested that this factor could play a significant role in the design of the Rufous-collared Sparrow song (Nottebohm 1975, 1985). Thus, the greater interindividual separation in open areas could favor the use of songs with lower frequencies, because they attenuate less with distance when broadcast at a height greater than one meter above the ground (Morton 1975, Marten and Marler 1977, Marten et al. 1977). In addition, greater interindividual distances could favor the use of songs with greater TRINT and slow-modulated whistled-like trill notes, because they accumulate less echos with distance (Wiley and Richards 1978). Second, there are strong and prevalent winds in open areas (but not in the woodland) from southwestern Buenos Aires Province which could influence song design. Up to now, we do not know whether this factor is related to the use of longer TRINT and lower frequencies in the grassland, but it is interesting to note that the Rufous-collared Sparrow songs of another open and windy area such as the Atlantic coast of Patagonia also have longer TRINT ranging from 300 to 400 milliseconds (Nottebohm 1975).

Finally, we note that the existence of a positive relationship between TRINT and TRBAND replicates the finding of Handford and Lougheed (1991) for the range of trill interval below 200 milliseconds. There are, however, several differences in their PCA that must be noted. First, they worked on the mean values of song features from different sites rather than individual song values. Second, their PC1 is dominated by TRBAND, TRMAX and SOLEN instead of TRBAND, TRMIN and TRLEN. We can only speculate about the significance of this relationship among temporal and frequency variables of the trill, but it is possible that

TRINT and TRBAND covariate because of the influence of the habitats' acoustic properties.

In summary, the striking association between dialect distribution and vegetation suggests a causal role of habitat on the vocal evolution of the Rufous-collared Sparrow. The present results suggest, however, that population density and wind intensity and prevalence are also important for a complete understanding about the adaptive significance of song structure.

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AERIAL DISPLAY SOUNDS OF THE BLACK-CHINNED HUMMINGBIRD[1]

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Key words: Hummingbirds; courtship; displays; vocalizations; Trochilidae.

Remarkably little is known of the sounds produced by hummingbirds. Earlier work is descriptive, and there are few published sonograms (see Mirsky 1976, Wells et al. 1978, Baptista and Matsui 1979, Wells and Baptista 1979). Considerable debate concerns whether sounds produced during aerial displays are vocal, mechanical or both (Rodgers 1940, Wells et al. 1978, Baptista and Matsui 1979). The sources of dive sounds cannot be determined by ear, and visual inspection of sonograms can be inconclusive. In some cases, the structure and temporal pattern of the sounds could fit either category of sound production.

Aerial displays of many hummingbirds consist of repeated pendulum-like arcs or vertical oval flights performed by both sexes in some species and used in both territorial and courtship displays (Pitelka 1942, Banks and Johnson 1961, Stiles 1982). Sounds are generally produced at the base of the arc, directly above the other bird (See descriptions in Bent 1940).

Here we present a sonographic analysis of the sounds produced during aerial displays by the Black-chinned Hummingbird (*Archilochus alexandri*). We compare sonograms of aerial display sounds to sonograms of mechanical and vocal sounds produced by Black-chinned Hummingbirds in other contexts. In addition, we compare Black-chinned Hummingbird display sounds to published accounts of the aerial display sounds of the Anna's Hummingbird (*Calypte anna*) and Costa's Hummingbird (*Calypte costae*), which are closely related to the Black-chinned Hummingbird (Mayr and Short 1970). Based on these analyses, we suggest the vocal source of the dive sounds of the Black-chinned Hummingbird.