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### Song characterization in the spectacled warbler (*Sylvia conspicillata*): a circum-Mediterranean species with a complex song structure

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## Song characterization in the spectacled warbler (*Sylvia conspicillata*): a circum-Mediterranean species with a complex song structure

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The spectacled warbler (*Sylvia conspicillata*) is a small passerine with a patchy distribution throughout the circum-Mediterranean region, including the North Atlantic archipelagos of Madeira, Canary Islands and Cape Verde. Here we characterize the species song structure on the island of Fuerteventura, quantifying repertoire size, inter- and intra-individual spectrographic variation, to determine whether acoustic variation occurred within an island population. Male song display was organized in song bouts of a variable number of song phrases, which in turn were made up of 4–69 syllables. We classified syllable types to derive a measure of repertoire size (number of different syllables) per song bout, and then used rarefaction methods to calculate the estimated repertoire size for our population of males. Three categories of song bout length were considered in analyses: short song bouts of 10 phrases, average bouts of 19 phrases and long bouts of  $\geq 29$  phrases. The observed and estimated repertoire size per male (between 43 and 126 syllables per male) increased with song bout duration, although the relationship was not significant for the estimated values. To test whether songs could be individually specific, we measured 11 spectrotemporal parameters of the song. A discriminant analysis using these variables performed poorly in classifying songs to the individuals that uttered them, but we found less variation in the individual than in the population for three out of the 11 variables. These individually specific variables, involving the first or the most common syllable of the song, the trill, were the duration of the first syllable of the phrase, the duration and the dominant frequency of the trill syllable. Our study emphasizes the complexity of spectacled warbler songs, in which males continuously add novel syllables over the entire song bout. This complexity appears to be determined by individual innovation capabilities rather than by the behaviour of copying neighbour repertoires, since songs of close birds were not more similar than songs from far-away territories.

**Keywords:** acoustic differentiation; complex song; Fuerteventura; repertoire size; song characterization; *Sylvia conspicillata*

### Introduction

For several decades, the study of oscine passerine song has been an important area of investigation with implications in ethological research (Otter et al. 1999; Seddon and Tobias 2010; Hesler et al. 2011), neurological or cognitive studies of vertebrates (Leitner

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and Catchpole 2003; Berwick et al. 2011), evolutionary biology (Lynch and Baker 1994; Päckert et al. 2003) and taxonomy (Schottler 1993; Bergmann and Schottler 2001; Raposo and Höfling 2003). Aspects of song learning have been in fact compared to language learning strategies in humans (Doupe and Kuhl 1999; Jarvis 2004). Birdsong has also served as a model for studying speciation processes, since divergent character displacement in song features, which in oscines are learned, can occur faster than in traits that depend on genetic changes (Lynch 1996; Collins et al. 2009; Marova et al. 2009; Grant and Grant 2010; Weir and Wheatcroft 2011). Acoustic differences may precede genetic processes and advance the detection of isolation processes when undergoing a cultural process of transmission (Grant and Grant 1996, 1997; Laiolo 2010). Indeed, birdsong may become a good indicator of incipient speciation between populations, acting as a prezygotic isolation mechanism (Grant and Grant 1996, 1997, 2007; Slabbekoorn and Smith 2002; Weir and Wheatcroft 2011).

Local dialects, i.e. geographic variants of the song of a species, are very common in oscine passerines and may be due to deterministic or stochastic forces. Among the former, natural selection may lead to acoustic adaptations to the local environment (Slabbekoorn and Smith 2002; Derryberry 2009) or, indirectly, affect the morphometric differentiation of populations, which in turn would influence the song spectrotemporal features constrained by body size and shape (Ryan and Brenowitz 1985; Podos 2001; Huber and Podos 2006). Ultimately social selection, driven by population dynamics or interspecific interactions, may also contribute to propel local song differentiation (Laiolo et al. 2008; Grant and Grant 2010).

Natural and anthropogenic barriers can favour vocal differentiation in passerine species and prompt isolation processes (Laiolo 2010). To determine the spatial scale at which acoustic changes become noticeable and biologically significant it is important to understand the mechanisms promoting isolation and evolutionary diversification (Kirschel et al. 2011). Here, we study song differentiation within a population of the spectacled warbler (*Sylvia conspicillata*), a small (~9 g weight) Palearctic passerine that has disjunct populations in the Mediterranean Basin and the North Atlantic archipelagos (Canaries, Cape Verde and Madeira; Cramp 1992). Although a great deal of research has been carried out with some common species of the Sylviidae family, such as *Acrocephalus melanopogon* (Fessl and Hoi 2000; Catchpole and Slater 2008), *Sylvia atricapilla* (Hoi-Leitner et al. 1995; Collins et al. 2009), *Sylvia communis* (Balsby 2000) and *Sylvia curruca* (Klit 1999), information is scarce on the majority of species of this highly vocal group of birds. The song of the genus *Sylvia* is known to play an important role in the development of reproductive barriers and, therefore, in differentiating populations (Brambilla et al. 2008). The spectacled warbler inhabits open habitats with sparse xerophytic bushes from the coast to over 2000 a.s.l. in Tenerife (Cramp 1992). In mainland Spain the species is considered a medium-distance migrant, wintering in the pre-Saharan range (Tellería et al. 1999), whereas North Atlantic (named Macaronesian) populations are sedentary (Cramp 1992; Martín and Lorenzo 2001). Despite its patchy distribution, only two subspecies have been described: *Sylvia conspicillata conspicillata* occurs around the Mediterranean Sea and *S. c. orbitalis* is restricted to Macaronesia. The latter is the model for this study.

Our aim was first to describe the physical characteristics of the spectacled warbler's song, as well as its repertoire size, which are poorly known. Then, we focus on the pattern of song variation to investigate (1) whether the acoustic features vary among and within individuals; (2) whether there are individual specific acoustic features; (3) whether song dissimilarities among individuals vary with the geographic distance between their territories. We expect that some song features permit individual identification, since the species may

sing from dense vegetation, where visual cues are hindered (Peake et al. 1998; Laiolo and Tella 2006). We also expect that song differentiation increases with distance and isolation among individuals, in line with results obtained with other oscine passerines in which males learn songs from neighbours (McGregor and Krebs 1989; Ellers and Slabbekoorn 2003).

## Material and methods

### *Study species*

Although the species can be heard throughout the year, the male's territorial song is uttered during the breeding period (Cramp 1992), as occurs in the lesser whitethroat *Sylvia curruca* (Klit 1999). The song can be described as a treble warble, organized in short and rapid phrases, composed of several syllables of varying length and bandwidth, usually alternating with three types of brief motifs: twitter, ticking and rattle (Cramp 1992). When there are conspecifics around the territories, song can be more intense and males also often emit a warning or alarm call, which is a full-throated metallic 'trrrrrr' that we have defined as a trill. Trill-like syllables also appear in male song phrases, in the form of several short ( $\sim 0.17$  ms) units repeated that sometimes vary in duration and intensity. Males sing from the top of perches but sometimes they display flight songs. In this paper we only considered the song produced from a perch since it is more common and tends to be longer (i.e. composed of more song phrases) than the flight songs (J.C. Illera, pers. obs.), thus permitting longer recordings per individual male.

### *Study area*

Our study was carried out on Fuerteventura (Canary Islands, Figure 1), which is the second largest island of the archipelago ( $\sim 1600$  km<sup>2</sup>). Fuerteventura has a semi-arid climate (Illera and Díaz 2006), a largely flat topography (mean altitude around 200 a.s.l.) and xerophytic vegetation dominated by sparse grasslands and dispersed shrub cover (Illera 2001; Seoane et al. 2010). These conditions are preferred by the study species (Martín and Lorenzo 2001), reaching mean densities of 0.4 birds/500 m<sup>2</sup> (Palomino 2005). Fieldwork was undertaken in January 2010, which corresponds to the peak of the breeding season (JC Illera, unpublished data).

Songs were recorded from 10–20 January 2010. Individuals were recorded at multiple localities in order to maximize the sampling of acoustic variability within Fuerteventura. Since males did not display at specific times of day, we were able to record songs both during the morning and the afternoon. The recording equipment consisted of a Marantz PMD660 Portable Solid State Recorder and a Sennheiser ME 67 microphone (frequency response 20–20,000 Hz  $\pm$  1.0 dB). Birds were recorded at close range (5–20 m), in open country. We recorded a mean of 4.72 minutes of song display per individual (range 1.2–10.26 min), since song bouts are short in this species (usually a few song phrases per bout are uttered, see below).

### *Spectrographic measurements*

We recorded 102.93 min of song from 27 birds. The mean number of phrases per individual during a song bout was  $21.8 \pm 3.32$  SE (range 3–77 phrases). In order to maximize both the number of individuals and the number of phrases analysed, we centred spectrographic measurements on 14 individuals that were recorded in good conditions (low noise-to-signal ratio), which uttered a minimum of 19 phrases during a single song

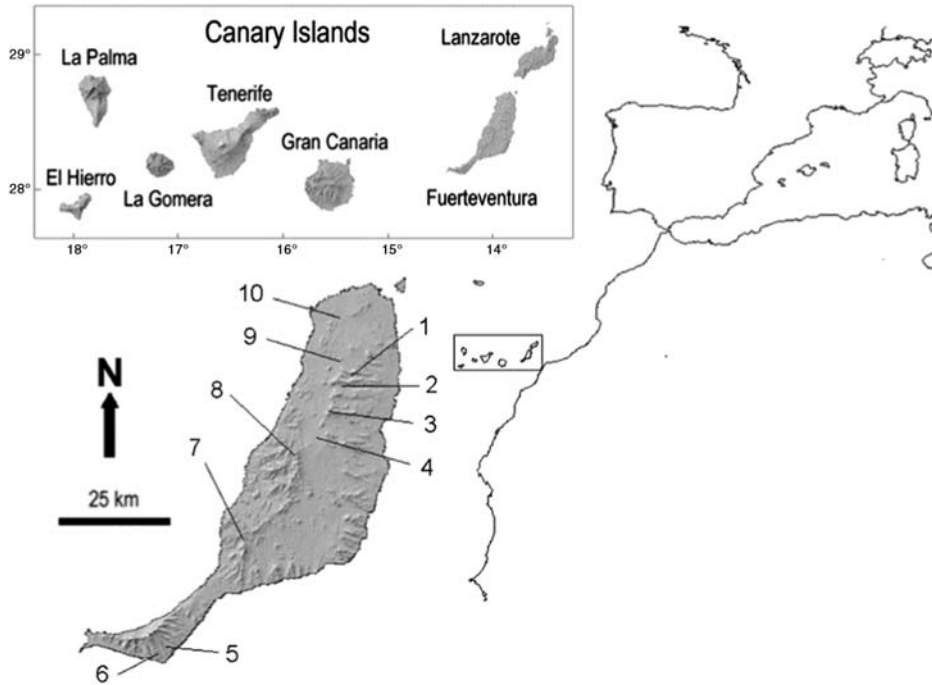


Figure 1. Map showing the localities studied in Fuerteventura. 1, Vallebrón; 2, Guisgüey; 3, Tetir; 4, Antigua; 5, Barranco Los Canarias; 6, Barranco de Esquinzo; 7, Barranco de Chilegua; 8, Betancuria; 9, Malpaís de la Arena; 10, Majanicho.

bout. This value approximately corresponds to an ‘average’ song bout in this population. On the other hand, estimates of song repertoires were based on 18 individuals that emitted from 10 to 30 phrases. In these analyses, we therefore considered a first group of four individuals uttering short song bouts (i.e. made up of 10 phrases), a second group of 10 uttering medium song bouts (19 phrases) and a third group of four individuals with long song bouts (29 and 30 phrases). Sound analyses were made using the software Avisoft SASLabPro (Raimund Specht, Berlin, Germany), with a Fast Fourier Transform (FFT) (sampling frequency 22,050 Hz, FFT length 512, time resolution 17.9 ms, frequency resolution 43 Hz and Bartlett Window Function). We measured temporal and frequency variables from the displayed waveforms and mean spectra of phrases, respectively, to quantitatively describe the species’ song (Figure 2). The parameters measured were: duration of the song phrase, *DurPhr*; the lowest frequency of the song phrase, *Fmin*; the maximum frequency of the song phrase, *Fmax*; the dominant frequency in the song phrase (i.e. the frequency band with the highest intensity), *Fdom*; the duration of the first syllable of the song phrase, *DurSyl*; the lowest frequency of the first syllable, *FminSyl*; the maximum frequency of the first syllable, *FmaxSyl*. In addition, we measured two features of the commonest syllable of the song (see below): the duration of a trill syllable, *DurSylTr*, and the dominant frequency of the trill syllable, *FdomTr* (Figure 2). We measured duration and frequency parameters of the syllables that were shared by all individuals (trill, first syllable), to test for interspecific differences in acoustic parameters at the syllable level (*DurSyl*, *FminSyl*, *FmaxSyl*, *DurSylTr*, *FdomTr*), as well as at the phrase level (*DurPhr*, *Fmin*, *Fmax*, *Fdom*).

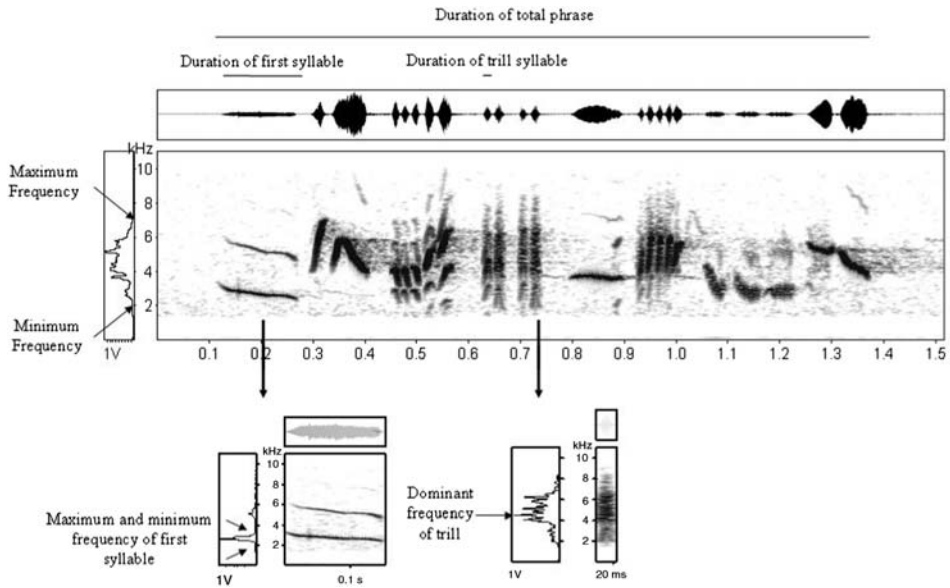


Figure 2. Song spectrogram of a spectacled warbler male.

Song complexity and song continuity were expressed in terms of number of original syllables per phrase, OrSyl, and total number of syllables per phrase, TotSyl, respectively (see below).

**Syllable classification**

The overall repertoire size was estimated as the number of different syllables uttered per song bout. Syllables were classified on the basis of structural characteristics by visually inspecting sonograms. We classified each syllable per phrase per individual and built a library of syllables for each individual. We considered a ‘syllable’ as a continuous stroke or collection of strokes separated by less than 25 ms on the spectrogram (in keeping with Briefer et al. 2008). To be considered as the same syllable, the matching portions had to be similar in timing, frequency and shape (either trill-like, tonal, with increasing, decreasing or constant pitch syllables). A phrase was considered as a sequence of syllables; phrases were separated by longer pauses than inter-syllable intervals ( $2.34 \pm 0.97$  SD seconds,  $N = 14$  individuals). Although syllable classification by eye may appear subjective (Lynch 1996; Garamszegi et al. 2005), it creates no more errors than other estimation techniques (see Botero et al. 2008). Nevertheless, in order to test the robustness of our classification and inter-observer repeatability and reliability of counting sonograms by eye (Jones et al. 2001), an initial approximation of syllable classification was made in 187 phrases from 10 different individuals independently by two observers (A. Palmero and P. Laiolo). Since we found a significant correlation between the two estimates of repertoire size (Spearman’s test, entering all song phrases,  $R_s = 0.708$ ,  $N = 187$ ,  $p < 0.001$ ; Spearman’s test with individual means,  $R_s = 0.976$ ,  $N = 10$ ,  $p < 0.05$ ), we can reasonably argue that our repertoire estimates are repeatable, and the inter-observer bias is limited in this study. In the following analyses, we only use the classification obtained by one of us (AP).

### Data analysis

#### *Estimates of individual repertoire size*

By using the observed repertoire size per song bout, we estimated the overall repertoire size of males by means of accumulation curves and Clench Equation (Soberón and Llorente 1993; Fagan and Kareiva 1997; Moreno and Halfpeter 2000), whose mathematical expression is:

$$S_n = a \times n / (1 + b \times n)$$

where  $S_n$  is the mean number of syllables at the  $n$ th phrase,  $n$  is the number of phrases observed at this point,  $a$  is the increase rate of new syllables at the beginning of the inventory, and  $b$  is a parameter that affects the shape of curve and represents the accumulation of new syllables during successive sampling of species repertoires.

In order to determine how song bout length could affect our estimates, we considered three categories of male song bouts, differing in length (phrase and syllable number). We took into account individuals uttering short song bouts (i.e. made up of 10 phrases,  $N = 4$  individuals), medium song bouts (19 phrases,  $N = 10$  individuals) and long song bouts (29 and 30 phrases,  $N = 4$  individuals). Repertoire size was estimated for each of the individuals in the different categories (short, medium and long song bouts), to test whether repertoire size estimates improved with increasing number of phrases sampled. For each individual, the equation was adjusted by means of the Simplex and Quasi-Newton algorithm. This equation assumes that the probability of adding syllables to an individual's repertoire increases over time (Hortal and Lobo 2005) and decreases with the number of syllables previously recorded (Soberón and Llorente 1993; Fagan and Kareiva 1997; Moreno and Halfpeter 2000). With this approach we obtained the estimated repertoire size and the estimated appropriate sample size (Lamas et al. 1991; Soberón and Llorente 1993; Gotelli and Colwell 2001). To avoid the influence of the order in which syllables appeared in the repertoire, since a set of data could lead to a family of curves depending on the order of the samples (phrases in our case) (Jiménez-Valverde and Hortal 2003), we first randomized the order sampling schemes 500 times using EstimateS version 8.2 (Colwell 2009), then we estimated the overall repertoire size of males using accumulation curves and the Clench equation as stated above. The repertoire was considered complete when the curve slope approached (or was lower than) 0.1 (Jiménez-Valverde and Hortal 2003).

#### *Acoustic variation between individuals and relationship with repertoire variation*

All analyses were made on 14 individuals, i.e. those uttering average and long song bouts, as described earlier. Acoustic measurements were taken from 19 phrases per individual, to maximize the number of individuals as well as the number of phrases analysed.

We used three methods to measure the degree of individuality in song features: the degree of individual coding (PIC) calculated from the coefficient of variation (CV); Kruskal-Wallis ANOVA on each song variable separately; and discriminant function analyses (DFA) considering the whole set of variables.

The coefficient of variation ( $CV = SD/\text{mean} \times 100$ ) was used to measure song stereotypy between and within individual repertoires (Bretagnolle and Lequette 1990; Lehner 1998). A prerequisite for individual recognition among the birds is that variation must be greater among individuals than within individuals (Jones et al. 1987). We calculated the CV for each acoustic parameter within then between individuals. A measure of call individuality was obtained from the ratio  $CV_b/CV_{i,\text{mean}}$  ( $CV_b = CV$  between individuals;  $CV_{i,\text{mean}}$



= CV mean value within individuals), which expressed the potential of individual coding (PIC) per parameter (Robisson et al. 1993; Seddon and Tobias 2010). A PIC value greater than one for a given parameter suggests that it may be useful for individual recognition, because intra-individual variability is less than inter-individual variability. When the value reaches 2, it is assumed to vary enough to permit recognition by females (Vignal et al. 2004).

Individual distinctiveness of male songs was also analysed using Kruskal-Wallis ANOVA, testing whether males differed significantly in their song acoustic features. A discriminant function analysis (DFA) was used to evaluate the extent to which the individuals' phrases could be assigned to the correct individual on the basis of all variables measured (standardized to zero mean and unit standard deviation), using cross-validation to estimate error rates. We generated a discriminant function by with-holding half of the phrases of each individual and then classifying the rest of the phrases. Using the cross-validation method we avoided the bias due to constructing discriminant functions with the same observations that are then classified *a posteriori* (Tobias and Seddon 2009).

In addition to previous analyses that involved parameters measured at the phrase level, we also ran chi-square goodness of fit tests to know if individuals differed between each other in the frequency of the four most common syllables uttered.

#### *Acoustic variation in space*

We used dissimilarity matrices and Mantel's tests to test whether song divergence was associated with geographical distances between individuals. Song dissimilarity was calculated in terms of Euclidean distances between the acoustic features measured (first matrix) or repertoire (second matrix) of bird pairs. We first built an initial matrix of Euclidean distances using the spectrotemporal features of the songs of 14 individuals (matrix size =  $14 \times 14$ ). A second matrix was built with the Euclidean distances of syllable abundance between individuals (matrix size =  $14 \times 14$ ). These two matrices were then compared with pair-wise geographical distances between each bird pair by Mantel's tests.

Statistical analyses were made with R 2.12 (R Development Core Team 2010), Statistica 7 and SPSS version 15.0. When variables did not match a normal distribution, non-parametric tests were used. Accumulation curves were calculated using the software EstimateS v. 8.20 (Colwell 2009).

## **Results**

### *Estimates of individual repertoire size*

We analysed a total of 316 phrases in 18 individuals. The estimated repertoire size in the three categories was consistently greater than observed (Table 1). However, these size differences were lower after increasing the number of phrases in song bouts, and were only recorded in the observed repertoire size (Table 1).

The observed repertoire size per individual was 33–67 syllables, and the estimated repertoire size was 42.69–126.21 syllables (Table 2). The number of new syllables appearing during a song bout did not reach an asymptotic value in any of the individuals analysed; i.e. the slope was greater than 0.1, varying between 0.33 and 2.02 (Table 2 and Figure 3), thus repertoires do not appear to stabilize within a song bout. However, around 70% of estimated individual repertoire was observed and in all the individuals a good fit for the repertoire observed was obtained (percentage of explained variance  $\geq 0.98$ ) (Table 2).

The mean repertoire size per song phrase per individual was not significantly associated with the overall observed ( $R_s = 0.30$ ,  $p = 0.29$ ,  $N = 14$ ) and estimated ( $R_s = 0.04$ ,

Table 1. Mean ( $\pm$  SD) observed (Obs.) and estimated (Est.) repertoire size and proportion between the two variables. Differences between observed and estimated repertoires among categories were tested with Kruskal-Wallis ANOVAs. The increase percentage represents the percentage of observed syllables appearing in the estimated repertoire.

	<i>N</i> = Individuals	Obs. Repertoire	Est. Repertoire	Increase percentage
1. Short song bout	4	41.00 $\pm$ 6.58	62.73 $\pm$ 15.86	52.99%
2. Medium song bout	10	50.40 $\pm$ 11.94	72.33 $\pm$ 25.65	43.50%
3. Long song bout	4	60.75 $\pm$ 5.44	79.14 $\pm$ 10.64	30.28%
Differences	1 vs. 2	$\chi^2 = 1.82, p = 0.18$	$\chi^2 = 0.50, p = 0.48$	
	2 vs. 3	$\chi^2 = 2.01, p = 0.16$	$\chi^2 = 0.98, p = 0.32$	
	1 vs. 3	$\chi^2 = 5.33, p = 0.02$	$\chi^2 = 2.08, p = 0.15$	

$p = 0.89, N = 14$ ) repertoire size (during a whole song bout). However, an outlier analysis found that one individual had a deviation of 1.9 in the standardized residuals of the observed regression trend, and after removing the correlation between the observed overall repertoire size and mean phrase repertoire size turned out to be significant (Pearson's correlation:  $R = 0.33, p = 0.04, N = 14$ ). This result suggests that there was a tendency for individuals with the most diverse phrases to also utter the most diverse song bouts.

#### *Acoustic variation between individuals*

We obtained PIC (Potential of Individual Coding) values greater than one in the variables DurSyl (2.12), DurTr (1.17) and FdomTr (1.12). Lower PIC values were found for Fmin,

Table 2. Values of repertoire size for individuals uttering song bouts of different length (10, 19, 29–30 phrases). Phrases, phrases in song bout; Obs. Rep, observed repertoire; Est. Rep, estimated repertoire; PER, proportion of the estimated repertoire observed in the phrases studied; PH, phrases that the species should utter to reach 95% of repertoire; Slope, slope at the last phrase for individuals in the study sample; a, values of parameter *a* in the Clench function; b, values of parameter *b* in the Clench function. All the curves presented  $R^2 \geq 0.98$ .

Individuals	Phrases	Obs. Rep.	Est. Rep.	PER	PH	Slope	a	b
15	10	40.00	62.22	0.64	110.99	1.45	10.65	0.17
16	10	42.00	61.07	0.69	88.41	1.32	13.12	0.21
17	10	49.00	83.17	0.59	133.38	2.02	11.84	0.14
18	10	33.00	44.45	0.74	72.57	0.89	11.64	0.26
1	19	37.00	45.58	0.81	100.45	0.41	8.62	0.19
2	19	35.00	42.65	0.82	90.90	0.36	8.91	0.21
4	19	49.00	74.51	0.66	192.96	0.89	7.34	0.09
5	19	52.00	72.65	0.72	147.94	0.79	9.33	0.13
7	19	57.00	82.14	0.69	166.99	0.93	9.35	0.11
9	19	58.00	76.30	0.76	116.54	0.74	12.44	0.16
10	19	37.00	45.56	0.81	98.77	0.40	8.76	0.19
12	19	67.00	94.82	0.71	148.91	1.03	12.1	0.13
13	19	45.00	62.85	0.72	153.87	0.69	7.76	0.12
14	19	67.00	126.24	0.53	326.14	1.66	7.35	0.05
3	30	53.00	64.63	0.82	132.42	0.33	9.27	0.14
6	29	64.00	82.39	0.78	170.22	0.51	9.16	0.11
8	30	65.00	90.01	0.72	222.59	0.61	7.68	0.08
11	30	61.00	79.54	0.77	189.75	0.50	7.96	0.1

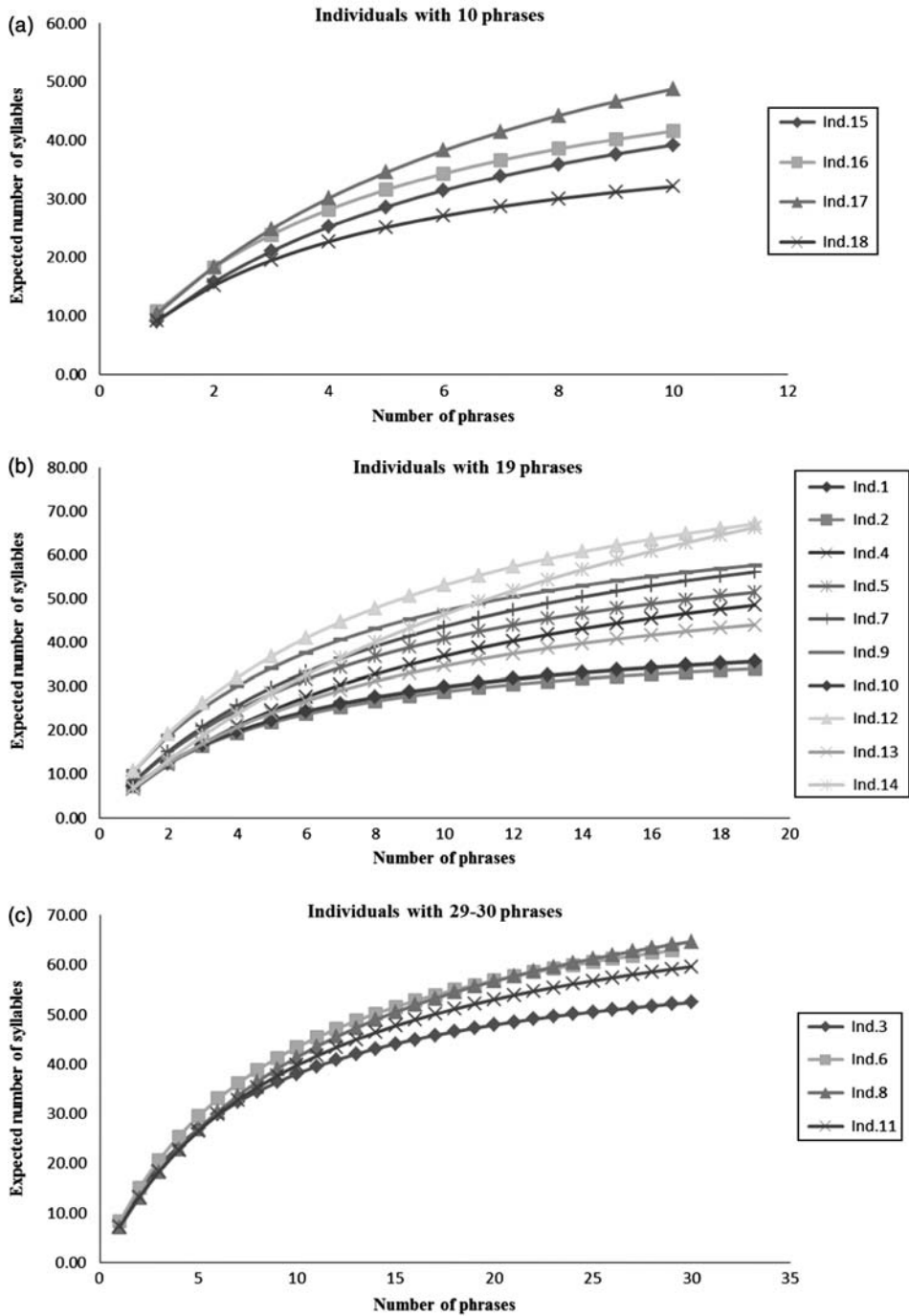


Figure 3. Saturation curves of the three categories analysed: (a) four individuals with short song bouts; (b) 10 individuals with medium song bouts; (c) four individuals with long song bouts.

Fdom, FminSyl and OrSyl. The remaining parameters reached values close to one (1.01), suggesting that these variables varied similarly within and among individuals.

Non-parametric ANOVAs highlighted significant differences in all parameters measured (Table 3). The DFA extracted three functions that significantly discriminated individuals ( $p < 0.001$ , in all functions), explaining 67.4% of the variability in the data set. These three functions were significantly associated with Fmax, FdomTr and DurSylTr, respectively (Tables 4 and 5). The percentage of correct classification was, however, very low: cross-validation assigned only 28.4% of phrases to the individuals uttering them (range 0–57.1%).

Although individuality was only slightly perceptible through the spectrotemporal variables considered, we found a significant difference between individuals in the frequency of use of the most common syllables (in all cases  $\chi^2 > 29.82$ ,  $p < 0.005$ , see Table 6).

### Acoustic variation in space

Mantel's tests showed that acoustic dissimilarity or repertoire dissimilarity did not increase with geographical distance (spectrotemporal variables versus distance:  $R = 0.07$ ,  $p = 0.33$ ; repertoire versus distance:  $R = 0.04$ ,  $p = 0.43$ ).

Table 3. Values of Potential Individual Coding (PIC) and Kruskal-Wallis analyses for each parameter measured. \*\*\*  $p < 0.001$ . DurPhr, duration of the song phrase; Fmin, the lowest frequency of the song phrase; Fmax, the maximum frequency of the song phrase; Fdom, the dominant frequency of the song phrase; DurSyl, the duration of the first syllable of the song phrase; FminSyl, the lowest frequency of the first syllable; FmaxSyl, the maximum frequency of the first syllable; DurSylTr, the duration of a trill syllable; FdomTr, the dominant frequency of the trill syllable; OrSyl, number of original syllables per phrase; TotSyl, total number of syllables per phrase.

	PIC	$\chi^2$
DurPhr	1.01	73.04***
Fmin	0.99	51.19***
Fmax	1.01	81.47***
Fdom	0.29	47.07***
DurSyl	2.15	60.13***
FminSyl	0.93	70.30***
FmaxSyl	1.05	56.11***
DurSylTr	1.17	69.33***
FdomTr	1.12	45.49***
OrSyl	0.99	61.27***
TotSyl	1.01	65.49***

Table 4. Statistics of the first three canonical discriminant functions used in the analysis.

Function	Eigenvalue	% Variance explained	Cumulative variance (%)	Canonical correlation
1	2.10	31.8	31.8	0.82
2	1.31	19.9	51.7	0.75
3	1.04	15.8	67.4	0.71

Table 5. Correlations of the spectrotemporal variables with the three discriminant functions extracted by DFA. Fmax, the maximum frequency of the song phrase; FdomTr, the dominant frequency of the trill syllable; DurSylTr, the duration of a trill syllable; DurSyl, the duration of the first syllable of the song phrase; Fmin, the lowest frequency of the song phrase; FmaxSyl, the maximum frequency of the first syllable; FminSyl, the lowest frequency of the first syllable; OrSyl, number of original syllables per phrase; DurPhr, duration of the song phrase; TotSyl, total number of syllables per phrase; Fdom, the dominant frequency of the song phrase.

	1	2	3
Fmax	0.59	0.24	0.31
FdomTr	0.17	0.57	-0.04
DurSylTr	0.47	-0.10	0.75
DurSyl	0.26	-0.03	0.12
Fmin	0.30	0.25	0.02
FmaxSyl	0.16	0.16	-0.32
FminSyl	-0.28	0.40	0.16
OrSyl	-0.10	-0.11	0.05
DurPhr	-0.09	-0.18	0.17
TotSyl	0.02	-0.23	0.14
Fdom	0.08	0.31	0.00

Table 6. Minimum (Min) and maximum (Max) frequencies of use of the four most frequent syllables in spectacled warbler songs.

	Trill (most frequent)	2nd most frequent	3rd most frequent	4th most frequent
Min	2.61	0.32	0.25	0.24
Max	55.83	3.70	6.78	3.52

## Discussion

### *Repertoire size*

We found that on increasing the number of phrases analysed, both the observed and estimated repertoire size increased, which is expected to happen in ‘virtuoso’ species (i.e. those with large repertoire size and great innovation capabilities, Garamszegi et al. 2005). Although no individuals reached the asymptote and stabilized their repertoire (slope more than 0.1), our results suggest that increasing the sample of phrases improves the estimates and slows down the increase in repertoire size with sampling effort (Figure 3). This finding confirms that a large sample size is very important to analyse repertoire size in songbirds (Garamszegi et al. 2005; Botero et al. 2008), and suggests that more effort has to be made to improve our estimates, possibly based on multiple recordings of the same banded individuals in several song displays during the breeding season. A larger sample size would have likely yielded a larger observed repertoire size, since longer song bouts resulted in more complex repertoires in our study species.

The repertoire size per song bout in the spectacled warbler was 33–67 (observed value) and 42.69–126.21 (estimated value) different syllables. This is a large repertoire according to Beecher and Brenowitz (2005). In passerines whose songs are best known, the repertoire size tends to be small (less than five syllables in *Parus major*) (McGregor et al. 1981) or moderate (around ten syllables, such as *Melospiza melodia*) (Beecher and Brenowitz 2005). The largest repertoires described so far have been described in *Alauda arvensis* ( $341 \pm 21$  syllables, Briefer et al. 2008), *Sylvia communis* (370–600 syllables,

Balsby 2000), and especially in *Turdus merula* and *Mimus polyglottos* (around 1000 syllables, DeVoogd et al. 1993). Considering our sample size and the lack of knowledge about the structure of the spectacled warbler song, the estimation of repertoire size by curve fitting with the Clench equation adjusted by the Simplex and Quasi-Newton algorithm was probably one of the best options, since capture–recapture methods produce more pronounced sample size effects on the magnitude of the estimates (Botero et al. 2008). Therefore, although repertoire estimates based on rarefaction analyses could produce unrealistic measures of song repertoire size in nature (Botero et al. 2008), we can conclude that the spectacled warbler's song is complex and diverse.

Since rarefaction methods in ecology were not developed to estimate repertoire sizes in species with complex repertoires and high innovation capabilities, they may provide an erroneous interpretation because they are based on the assumption that a plateau has to be reached, while apparently no syntactic structure appears within songs (i.e. syllables are randomly associated, see also Peshek and Blumstein 2011). When species are innovating to a great extent in their songs, and their syllables have a poor repetition rate, repertoires become dynamic entities in which syllable structure is continuously shifting. In our study, the most common syllable, the trill, made up 38.3% of the total repertoire, but the other syllable types had a very low repetition rate (6.92% for the second most common syllable and 1.85% for the third, although most of the syllables constituted less than 1% of the whole repertoire).

The overall repertoire sizes (song complexity) were not significantly correlated with the repertoire of each phrase (phrase complexity), although the trends turned out to be significant on removing one extreme case. Regardless of the fact that greater sample size could help to shed light on this relationship, our findings suggest that there is a slight tendency for complex songs to be made up of complex song phrases. In this context, the repertoire size within song phrases could be considered as an indicator of repertoire size on the scale of song bouts, thus revealing the complexity of the whole individual repertoire but requiring less effort to measure it.

### *Differences between individual songs*

Comparisons between individuals revealed significant differences in all the acoustic variables measured, although some variables defined individual identity better than others. Our PIC and discriminant analyses detected certain variables (duration of the first syllable of the song phrase, maximum frequency of the phrase, duration of a trill syllable, and dominant frequency of the trill syllable) that better code individual identity, i.e. they varied more between than within individuals and served to discriminate between them. These variables were preferably associated with specific syllables (first syllable, trill) rather than to phrase parameters (overall phrase duration and frequency range), suggesting that individuality in this species is achieved at a low level of song organization. Cross-validation poorly assigned songs to the individuals uttering them (the percentage of correct classification was as low as 28%), which suggests that the individuals do not have very strong specific individual spectrographic characteristics or phrase structures. In the study species, parameters measured at phrase level could well represent species- or population-specific characteristics, whereas the repetition rate and characteristics of syllables would characterize variation at a lower level, that of the individual. In fact, individuals did use syllables with different abundance (as occurs in species with elaborate songs, Garamszegi et al. 2005), the most common syllables being uttered in different proportions by the individuals sampled.

These results confirm that each individual sang different syllables, varying individually in syllable structure and order (Ruegg et al. 2006). Both univariate and multivariate analyses show that the variables associated with the trill have the potential to discriminate between individuals. Although the duration of the first syllable was the only parameter with a PIC value higher than 2, and therefore is supposed to be a strongly individual-specific feature (following Vignal et al. 2004, 2008; Seddon and Tobias 2010), it was not, however, among the three functions extracted by DCA. The duration and dominant frequency of the trill are the remaining parameters with potential for individual coding: both were highlighted by high PIC values (Table 3) and significant correlations with the first discriminant functions (Table 5). The trill being the most common syllable in the species' song, it could well be used to encode individual information. It is frequently repeated, and could be used by females or conspecifics as a rapid indicator of individual identity when the repertoire is very varied (Fessl and Hoi 2000; Garamszegi et al. 2005). Alternative explanations for this finding may take into account the function of the syllable. Since it is a component of the alarm-call and churr-call (Cramp 1992), the trill may be used in songs to warn neighbours and defend territories, and thus carry information about territory owners (Hesler et al. 2011).

Although playback experiments could better reveal if individuality is perceived by conspecifics (Lind et al. 1996), we can argue that the first song syllable is the first portion to be heard in an individual's song, therefore it could more rapidly code individual identity among neighbours than later ones, without requiring listening to the full individual repertoire. Increased individuality in the initial portions of vocalizations have been found in other bird species, such as the rufous collared sparrow *Zonotrichia capensis* (Nottebohm 1975; Laiolo 2011), the puget sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis* (Nelson and Poesel 2007), and the king penguin *Aptenodytes patagonicus* (Lengagne et al. 2000).

Spectacled warbler songs do not appear to be shared among the closest individuals. Mantel tests revealed no correlation between geographical distance and acoustic differentiation, indicating absence of acoustic sub-structure within Fuerteventura. These results contrast with studies showing more acoustic similarities among closely located birds than with individuals singing in remote territories, with a clear tendency to decrease with distance (Laiolo and Tella 2006; Franco and Slabbekoom 2009). This trend results from post-dispersal learning, i.e. a modification of the original repertoire when settling in new areas, through imitation of conspecifics (Briefer et al. 2008; Peter 1997; Franco and Slabbekoom 2009; Kelley and Healy 2011). The capability to combine different types of syllables increases the intra-individual variability, although when a song is learned by mimicking conspecifics a conservative influence within a population might exist, and acoustic dissimilarities should be lowest among neighbours (Lynch 1996; Hultsch and Todt 2004). Two hypotheses named 'Repertoire' and 'Sharing' have been proposed to explain song repertoire size. The former predicts that large repertoires are positively selected and females base their mate choice on this acoustic feature. The Sharing hypothesis predicts that males copying neighbours (i.e. singing local songs) are favoured by females, that is converging, rather than diverging from neighbours becomes the optimal strategy (Beecher and Brenowitz 2005). Maintaining individual stereotypy becomes more difficult when repertoire size is larger (Briefer et al. 2008), and this may be the case in the spectacled warbler system. It is possible that our sampling was not exhaustive, since the similarity between neighbours should be detected over shorter distances. However, it is also plausible that large and poorly repetitive song repertoires prevent effective sharing among neighbours, resulting in scarce differentiation over distance at the local level and scarce stereotypy at the group level as well

(Kroodsma 1974). The magnitude of spectacted warbler variation in repertoire size (inter-individual CV values), both observed (21.97) and expected (32.45), exceeds the magnitude of inter-male variation in ornamental traits in birds (Møller and Alatalo 1999), thus suggesting that larger repertoires in males might be an important trait selected by females, providing support for the Repertoire hypothesis (Beecher and Brenowitz 2005; Briefer et al. 2008).

The fact that the farthest birds were not more diverse than closer ones suggests that the Fuerteventura population is not structured on the basis of song features. The lack of geographical barriers for the species – this warbler is well distributed throughout the island (Trujillo 2007) – likely allows individuals to disperse over long distances, and song traditions to spread freely.

Despite the somewhat reduced sampling, this study shows that the spectacted warbler is a species with a complex repertoire, which appears to be constantly creating new song elements during song bouts. Individuals do not share song repertoires, and further studies are necessary to disentangle the possible causes of this. Potential explanations involve difficulties in memorizing complex songs, great territorial turnover, and selection pressures that favour innovation over copying to increase repertoire size. Individual identity is achieved through stereotypy of individual syllable types rather than through individual specific features of song phrases.

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