Information theory reveals that individual birds do not alter song complexity when varying song length

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The application of information theory to birdsong research provides insights into the internal organizational structure of the communication systems of nonhuman animals, which can be integrated with behavioural data. We applied information theory to test for trade-offs between two birdsong features, complexity and duration, which may be costly for the individual. We determined and quantified the internal structure of the song in a wild passerine, the spectacled warbler, *Sylvia conspicillata*, and tested for differences in song variability between song bouts of different lengths. We found (1) no correlation between song bout length and internal complexity, since song bouts of different durations presented the same degree of complexity, (2) a high potential for communication capacity because of the equilibrium between the unification and diversification of the song repertoire, and (3) a communication system that followed a first-order Markov chain with a high degree of variation and individuality, giving rise to a complex and highly variable song. The fact that both short and long songs showed high internal complexity suggests that no clear constraint exists between these features, and that the spectacled warbler may sing intrinsically complex songs throughout the display. This complexity is enhanced by the lack of sharing among individuals, which would otherwise homogenize songs and constrain individual innovation ability.

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Communication plays a central role in all aspects of individual life in animal communities, especially in higher vertebrate groups or eusocial insects, in which communication system complexity reaches an apex (Bradbury & Vehrencamp, 1998). Both solitary and territorial animals present elaborate signals with several functions, such as territorial defence, antipredator behaviour or mate attraction (Caro, 2005; Cuthill, Stevens, Windsor, & Walker, 2006; Gil & Gahr, 2002; Laiolo, Tella, Carrete, Serrano, & López, 2004). For these signals to be effective, they must follow certain rules that allow the transmitted information to be understood and consequent actions to take place, and whose flexibility to environmental conditions is dictated by memory and learning capacities (McCowan, Doyle, & Hanser, 2002).

One of the most studied nonhuman animal communication systems is birdsong (Doupe & Kuhl, 1999). Because of their vocal learning capacity, from an acoustic communication point of view,

birds can be equated with humans as are many primates, despite their phylogenetic differences (Berwick, Okanoya, Beckers, & Bolhuis, 2011; Nottebohm, 1970). Indeed, decades of birdsong studies have shown that birdsong (in oscine birds) shares behavioural, neural, genomic and cognitive similarities with human speech (Berwick et al., 2011). The complexity of birdsong has traditionally been evaluated using repertoire size, that is, the number of different sounds (syllables) uttered (Buchanan & Catchpole, 1997; Catchpole, 1986). In the 1970s, researchers began to apply information theory (Shannon, 1948; Shannon & Weaver, 1949) and Zipf's law for human language (Zipf, 1949) to the internal organization of birdsong (Lemon & Chatfield, 1973), to quantify the amount of information transferred by this kind of signal and to improve our understanding of the song's structure and its organizational complexity. These mathematical theories were developed to measure the amount of information transmitted in a communication system, in particular through telephone lines (Shannon & Weaver, 1949) and to describe human languages (Zipf, 1949), but both offered useful tools to study the existence of syntactical organization in complex animal communication systems (Briefer, Osiejuk, Rybak, & Aubin, 2010; Da Silva, Piqueira, &

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Vielliard, 2000; Da Silva & Vielliard, 2006; Haldane & Spurway, 1954; Hazlett & Bossert, 1965; McCowan et al., 2002; McCowan, Hanser, & Doyle, 1999). In addition to applications in mammals (e.g. bottlenose dolphins, *Tursiops truncatus*, and squirrel monkeys, *Saimi sciureus*, McCowan et al., 1999, 2002; humpback whales, *Megaptera novaeangliae*, Suzuki, Buck, & Tyack, 2006), information theory has also contributed to disentangling behavioural and ecological questions in birds, for instance in rose-breasted gros-beaks, *Pheucticus ludovicianus* (Lemon & Chatfield, 1973), white-vented violetears, *Colibri serrirostris* (Da Silva & Vielliard, 2006) and skylarks, *Alauda arvensis* (Briefer et al., 2010). These studies have revealed a high level of variability among species and ecological/ethological contexts.

It has been hypothesized that the development of large reper-toires is energetically costly (Buchanan, Leitner, Spencer, Goldsmith, & Catchpole, 2004; Catchpole, 1996), and time consuming, since singing time cannot be invested in other activities such as foraging (Oberweger & Goller, 2001). Therefore, individuals might face a song performance trade-off, either uttering long sig-nals with a simple internal structure or short and complex ones in order to achieve a cost−benefit balance. Alternatively, since bird-song is an honest signal of quality (Catchpole & Slater, 2008; Nowicki, Hasselquist, Bensch, & Peters, 2000), it is also possible that the highest quality individuals may utter longer and more complex songs, since such males must be more able to bear display costs (Chappell, Zuk, Kwan, & Johnsen, 1995; Oberweger & Goller, 2001). We have focused our study on these two alternative hy-potheses, using the spectacled warbler, *Sylvia conspicillata*, as a model. This species utters song bouts that differ in duration and repertoire size, and adds new syllables throughout the song bout

(Palmero, Illera, & Laiolo, 2012). Thus, this is a good species in which to test whether parameters derived from information theory that describe the internal organization and complexity of songs, such as redundancy, openness and entropy, vary according to the quantity (duration) and quality (repertoire size) of the song signal.

We compared the internal complexity of the phrases in in-dividuals uttering song bouts of different length by means of Markov chain analyses, Zipf's law, measures of versatility and repertoire sharing. We hypothesized that individuals with the longest song bouts and largest repertoire size should also show the greatest complexity in the internal structure of the song (in terms of entropy orders and versatility), because longer song bouts include more syllables and more transition patterns (syllables' succession order or sequences) in species with complex songs (Hamao, 2008). Furthermore, to determine the degree of shared information, and its spatial distribution in the population, we assessed the variation within and between individual sequences.

METHODS

Species, Study Area and Song Recording

The song of the spectacled warbler is organized into song bouts with a variable number of song phrases, composed of several syl-lables of varying length and bandwidth (Fig. 1; Palmero et al., 2012). We define a 'syllable' as a continuous stroke or collection of strokes separated by less than 25 ms, while a 'phrase' is a sequence of syllables, separated by longer pauses than intersyllables. The phrase lasts a mean ± SD of 1.58 ± 0.31 s and the interphrase pause lasts 2.34 ± 0.97 s in the study species (Palmero et al., 2012).
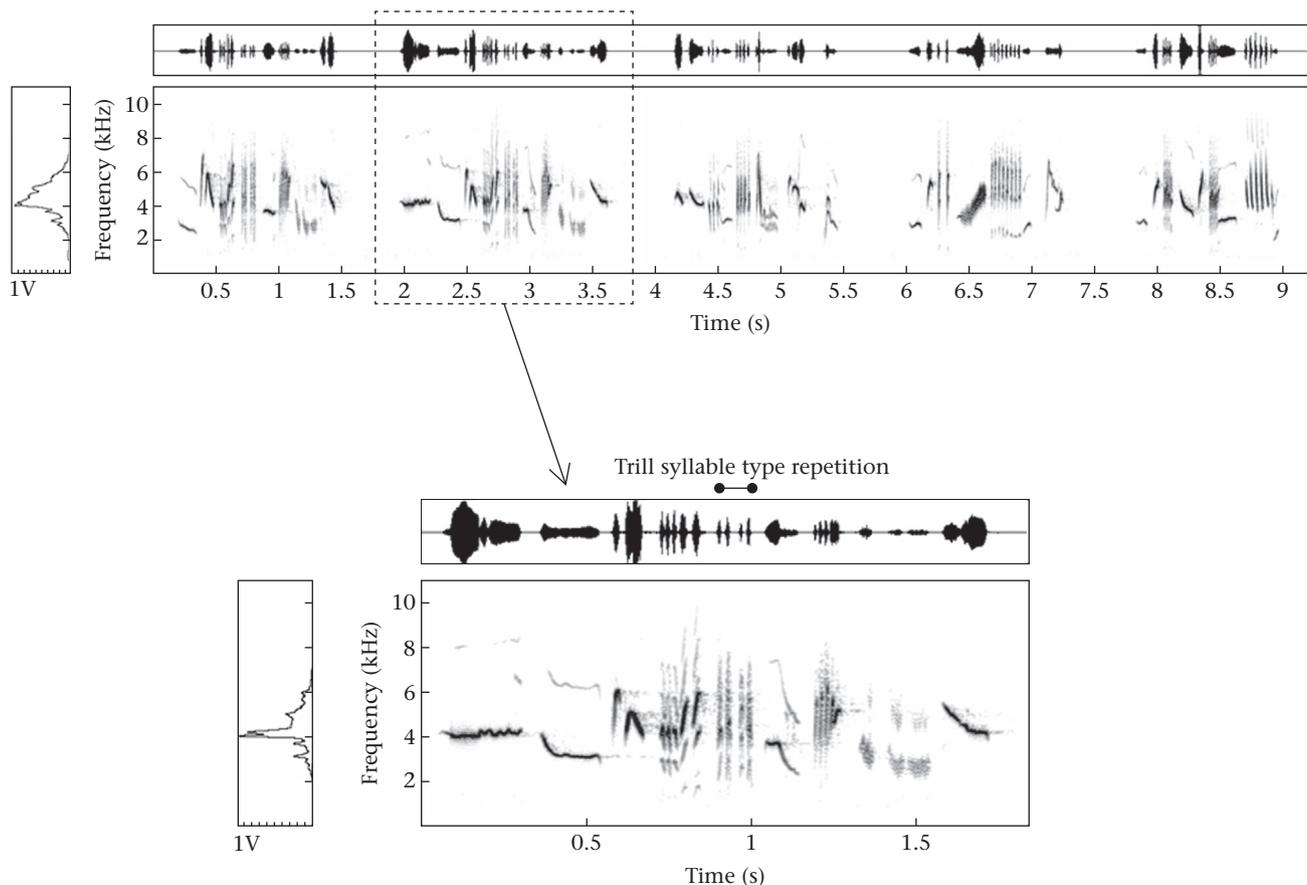
Figure 1. Portion of a song bout of a spectacled warbler male from Fuerteventura island. The interphrase time has been reduced to allow five consecutive phrases to be shown. A detail of one phrase with a trill syllable type repetition in the middle of the phrase is also shown.

The sampling was conducted in Fuerteventura, the second largest of the Canary Islands (ca. 1600 km^2), with a semiarid habitat characterized by a xerophytic and dispersal shrub community dominated by *Launaea arborescens*, *Euphorbia regis-jubae*, *Salsola vermiculata*, *Sueda* spp., *Lycium intricatum*, *Nicotiana glauca* and *Asparagus* spp. (Illera, 2001; Rodríguez, Garcia, & Reyes, 2000). The spectacled warbler is a sedentary and common breeding species throughout the island (Martín & Lorenzo, 2001), reaching mean densities of 0.4 birds/500 m^2 (Palomino, 2005). The breeding period seems to be mainly determined by rainfall, as occurs with other passerine species inhabiting Fuerteventura (Illera & Díaz, 2006), with a breeding peak after January (J.C. Illera, personal communication).

Vocalizations were recorded during 10–20 January 2010. We recorded individuals from 10 localities (distance range 2.4–77.8 km; Appendix Fig. A1) distributed throughout the island to account for the acoustic and internal organization variability within the island. We used a Marantz PMD660 Portable Solid State Recorder and a Sennheiser ME 67 microphone (frequency response 20–20 000 Hz, ±1.0 dB). Songs were recorded from sunrise to sunset.

Song Analyses and Song Duration Groups

We selected 18 individuals with good signal-to-noise ratios and song bouts of different durations. Songs were transferred to the computer and high pass filtered at 1000 Hz to eliminate background noise. The recordings were analysed 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).

To estimate the species repertoire, each syllable was classified on the basis of structural characteristics by visually inspecting sonograms, and was assigned a unique code (see Palmero et al., 2012 for further details). When the same syllable was found in different phrases or individuals it was identified with the same code. The observed repertoire was obtained for each male, and a high variability in repertoire size was found (from 33 to 67 syllables per male). Palmero et al. (2012) showed that the repertoire of the species can be potentially larger, but we are confident that this result does not affect our ability to assess the internal structure complexity and organization of the song. We sampled sufficient phrases and syllables per individual to apply the information theory approach to study the sequential combination of the syllables in the song, which is independent of the total number of different syllables uttered (Hailman, Ficken, & Ficken, 1985; McCowan et al., 1999; Shannon, 1948).

Individuals uttered song bouts of different lengths, which also differed in the number of syllables constituting them. We studied the complexity and the internal organization of songs (see below for their quantification) in three groups of individuals defined according to the number of phrases available per category and meaningful grouping based on the song length distribution in the species (Palmero et al., 2012): those uttering (1) short song bouts (10 phrases, average duration ± SD = 36.53 ± 1.94 s, $N = 4$ individuals), (2) medium song bouts (19 phrases, average duration ± SD = 73.33 ± 5.96 s, $N = 10$ individuals) and (3) long song bouts (29–30 phrases, average duration ± SD = 118.31 ± 11.42 s, $N = 4$ individuals).

Zipf's law to measure redundancy and diversity

Zipf (1949) formulated an algorithm (Zipf's law) that allows the evaluation and quantification of deviation between diversity and redundancy, as well as the openness of the communication system. Zipf's law is based on the 'Principle of Least Effort', which proposes that there must be a balance between unification and diversity in a language, such that the number of elements should not be so highly repetitive that the communication would be too simple, nor so heterogeneous that there would be too many possible combinations, and thus communication would be so complex as to inhibit memorization, utterance and clarity. Therefore, an efficient communication system should be one that expresses an appropriate balance between diversity and redundancy (neither too diverse nor too repetitive). We applied Zipf's law to estimate the randomness and potential capacity for transferring information in the spectacled warbler's song. We plotted the logarithm in base 10 of the frequency of syllable occurrence (from the commonest to the rarest) against the logarithm of its rank of use per individual (first, second, third, etc. syllable) and extracted the Zipf's slope or statistics (α) for each individual, to make an initial approximation of the structural composition of its repertoire (McCowan, Doyle, Jenkins, & Hanser, 2005). When the slope of the curve is lower than −1 there is more redundancy than diversity, and when it is between 0 and −1 there is more diversity than redundancy (McCowan et al., 1999). Values of −1 indicate that a balance exists between repetition and diversification, and the signal is neither too repetitive nor too diverse. Moreover, in this latter case it is assumed that a high potential capacity exists for transferring information such as occurs in human languages (McCowan et al., 1999). We compared the slopes of individuals belonging to different groups and tested for differences by means of ANOVAs.

Shannon theory and Markov chaining

According to the information theory of Shannon (1948) and Shannon and Weaver (1949), originally developed to measure the amount of information transmitted in a communication system, the amount of information is a measure of an individual's freedom of choice among the discrete units (symbols, syllables in the case of birdsong) available in a system when selecting a message to send. The amount of information is measured as 'entropy' (H) and is expressed as the probability of a symbol being chosen, and the probability of the next symbols being chosen. Entropy reaches its maximum value when all the symbols have the same probability of being chosen and drops to zero when a symbol has no possibility of being chosen, meaning signalling is constrained by internal rules. To assess whether there were differences in the internal organization of short, medium and long songs, we focused on the observed repertoire of syllables and the order of the syllables uttered through every phrase (sequence of syllables) during the song bout of each individual. We analysed the whole bout per individual to obtain the sequences of syllables, and from these we then estimated entropy orders. We did not join the last syllable of one phrase to the first syllable of the following phrase, because if song structure is present these syllables would belong to different phrases. We calculated entropy orders with the following formulas (Briefer et al., 2010; Lemon & Chatfield, 1973).

(1) Zero-order entropy, H0, estimates repertoire diversity, as $H0 = \log_2(k)$, where k is the observed repertoire size.

(2) First-order entropy, H1, estimates simple repertoire internal organization of the song uttered, as $H1 = -\Sigma P_i \log_2(P_i)$, where P_i is the probability of occurrence of each syllable in the song bout; it was calculated as the number of times we observed a syllable divided by the total number of syllables uttered.

(3) Higher-order entropy, Hn, estimates the complexity of song internal organization by quantifying the co-occurrence of different syllables, for instance syllable pairs (sequences of two syllables) and triplets (sequences of three syllables). This measure takes into account the probability that different syllables appear in the same sequence (joint probability) and the probability of occurrence of one syllable following another specific syllable (conditional probability). The formula of higher-order entropies is calculated as

follows: $Hn = -\Sigma P_{ij}\log_2(P_{j/i})$, where n is the order entropy; P_{ij} is the joint probability of the sequence of two syllables i and j. This is equal to the number of times that the ij sequence is observed, divided by the total number of two-syllable sequences in the song. $P_{j/i}$ is the conditional probability of j occurring when the previous syllable is i. It is calculated as the joint probability of sequence ij, divided by the probability of syllable i. When there are three syllables, the conditional probability is calculated as the joint probability of the sequence ijk divided by the joint probability of the preceding sequence (ij) and so on.

A sequence of syllables is produced according to certain probabilities. When the probabilities depend on the previous syllables uttered, this dependency is called a Markov process and is represented by chains of conditional probabilities (Markov chain), for example the probability distribution for the nth random syllable of one sequence depends on the ($n-1$) previous syllables. Therefore, the information contained in a sequence would be maximal if each syllable is totally independent of the preceding one; in this case all the syllables would have the same probabilities of occurrence.

According to this process, we can generate an 'information graph' (by plotting the values of entropy order against sequence size) to establish the degree of Markov chaining and the degree of dependency of the syllables constituting a sequence, which would allow the determination of the structure complexity in the song. To achieve this, we plotted the mean values of entropy (from H0 to H6) against sequence size per individual to obtain an information graph for each group of song bout durations. A sharp negative relationship in the graph indicates a great loss of information and the point where the slope changes marks the degree of Markov chaining of the song (Briefer et al., 2010; Lemon & Chatfield, 1973). We also plotted the slope values against the entropy transition (the change from one value of entropy order to the next) to identify accurately where the greater loss of information occurs, and to establish the degree of Markov chaining in the spectacled warbler's song.

To derive the parameters, we developed custom MatLab (MatLab R2011a, Mathworks, Inc., Natick, MA, U.S.A.) routines. These were used to scour the phrases and select the sequences compounded from two to six syllables after imputing the total repertoire (the codes of each syllable) and the phrases per individual. The program classified the sequences of different length in the bout of each individual, and calculated the frequencies of each syllable or sequence, joint and conditional probabilities and entropies. We took into account sequences of up to six syllables according to characteristics of the spectacled warbler's song and the sample size available. This size of sequences is comparable to that of other species with similar repertoire size (Briefer et al., 2010; Lemon & Chatfield, 1973).

We also calculated the relative entropy (RE) and redundancy (RD) for each entropy order per individual, to measure the proportion of free choice for generating sequences ($RE_n = H_n/H_0$), and the proportion of sequences that are not determined by free choice, but by statistical rules governing the use of syllables ($RD_n = 1 - RE_n$; it is reciprocal to RE; Briefer et al., 2010). Once we had the values per individual we calculated the mean values of all these measures per song bout group (the formulas we used are shown in Table 1).

Furthermore, we established the versatility of syllables in each individual (syllable type versatility), as the mean number of different syllables in a phrase divided by the total number of syllables in that phrase, and also the versatility in the pairs of each individual (pair type versatility) as the number of different sequences of two syllables (formed by different syllables), divided by the total number of pairs.

Differences in the internal organization of the song between individuals differing in song bout duration were tested by ANOVAs and t tests using SPSS version 13. Normality was checked by Kolmogorov–Smirnov tests and no variable needed to be transformed.

Song Sharing among Individuals

We analysed whether the sharing of syllables or pairs of syllables (sequences of two syllables) between individuals changed with the geographical distance between their territories (range 0.11–77.79 km, mean ± SD = 28.43 ± 21.69), focusing on the 14 individuals that were recorded for 19 consecutive phrases (to standardize the number of phrases analysed), in other words the 10 individuals with a medium song bout and the four individuals with a long song bout, but only considering their first 19 phrases. We quantified the repertoire sharing (RS) of the syllables and pairs using the following formula: $RS = Z/((X+Y)-Z)$, where X and Y are the total numbers of syllables or pairs uttered by individuals x and y, and Z is the number of syllables or pairs shared by the two individuals (Briefer et al., 2010; Hultsch & Todt, 1981). By estimating the differences between individuals in the repertoire sharing ($1-RS$), we constructed a dissimilarity matrix. We performed two Mantel tests using the software R version 2.13.2 (R Development Core Team, 2007) to test the relationship between the geographical distances (calculated from individual's coordinates) and the syllable sharing or pair sharing dissimilarity matrix. Significance levels were obtained with 99 999 permutations of the data set.

Finally, to assess whether individuals shared the most common syllables and pairs, we ordered syllables and sequences on the basis of their occurrence in the repertoire of each individual, and selected the 10 most common per individual to make pairwise comparisons between individuals and establish whether any syllable or pair was uttered exclusively by one individual.

RESULTS

For 18 individuals, we analysed 316 song phrases comprising 4–69 syllables each (mean ± SD = 18.55 ± 3.24 syllables per phrase) and totalling 6444 syllables. Depending on the song bout group to which each individual belonged, different numbers of phrases were analysed per individual (10, 19 or 30 phrases, see Table 2).

Zipf's Law to Measure Redundancy and Diversity

The Zipf's graphs showed a slope close to -1 in all the individuals, with values varying between -0.92 and -1.43 (Table 3, Fig. 2). These results indicate that all individuals were close to Zipf's

Table 1
Formulas of the parameters quantified in this study

Measure	Formula	Information obtained
Mean entropy order	$\overline{H}n = \frac{1}{M} \times \sum_{i=1}^{M} H_{in}$	Mean value of entropy order n for the M song bout group
Mean relative entropy	$\overline{RE}n = \frac{1}{M} \times \sum_{i=1}^{M} RE_{in}$	Mean proportion of the free choice building sequences for each entropy order n for the M song bout group
Mean redundancy	$\overline{RD}n = \frac{1}{M} \times \sum_{i=1}^{M} RD_{in}$	Mean of the fraction of the sequence structure determined by statistical rules governing the use of the syllables for the M song bout group

In the formulas n is the entropy order; M is the song bout group (short, medium and long) and i is the number of individuals in the M song bout group (short song bout = 10 phrases, medium song bout = 19 phrases and long song bout = 30 phrases).

statistics ($\alpha = -1$), and thus the species presented a balance between repetition and diversification, with a high potential capacity for communication and transfer of information. The lack of significant differences ($F_{2,15} = 0.73$, $P = 0.5$) between slopes of different song bout groups suggests that all individuals followed a similar pattern of redundancy/diversity regardless of the length of the signal. There was also no significant correlation between the Zipf's slope and the repertoire size (Pearson correlation coefficient: $r_{16} = 0.46$, $P > 0.05$).

Shannon Theory and Markov Chaining

The mean values of the entropy orders (H), relative entropy (RE) and redundancy (RD) for each group of individuals are shown in Table 4. In all individuals, while the entropy order increased, the entropy values decreased, such that the amount of information of the sequences decreased while their size increased. The RE1 values (Table 4) indicate that males have approximately 70.6% free choice of syllables when they build a sequence. This value of free choice decreased strongly at the level of sequences of two syllables (see RE2 values in Table 4) which means that the freedom of choice is much lower, so some pairs of syllables may be more common than others. The remaining RE values (RE3–RE6) decreased gradually. As RD values are reciprocal to RE, when the latter increased the former decreased, but the values of RD1 (Table 4) indicate that a certain amount of structure exists in the spectacled warbler's song, since around 29% of the syllable sequence uttered was not free choice. The t tests stressed differences between song bout groups in some entropy orders (H0, H2, H3 and H6, see Appendix Table A1), even after removing one individual (individual 3) that showed slight deviation from the remaining individuals in the entropy order values. None the less, all individuals, regardless of the song bout group to which they belonged, showed the same relative tendency according to the entropy order values: the amount of information lost in each level of entropy was similar although the net values were different, and the slope's variation in the information graph was very similar between groups (Fig. 3). The most negative slope values occurred between H1 and H2 (Fig. 3; Appendix Table A2, Fig. A2) except for the group of individuals uttering long song bouts, in which individual 3 presented a slightly lower slope value between H0 and H1. To determine Markov chaining, we performed the analysis by both including and excluding this individual from the data set. The information graph indicated that all individuals

Table 3
List of slope and R^2 values of Zipf's graph test for each individual

Zipf's law	Individual	Slope	R^2
Short song bout	15	−1.04	0.95
	16	−1.04	0.93
	17	−0.92	0.89
	18	−1.29	0.93
Medium song bout	1	−1.30	0.89
	2	−1.26	0.93
	4	−1.05	0.94
	5	−1.05	0.91
	7	−1.12	0.94
	9	−1.06	0.95
	10	−1.43	0.95
	12	−1.04	0.95
	13	−1.24	0.96
	14	−0.95	0.93
Long song bout	3	−1.27	0.92
	6	−1.22	0.95
	8	−1.02	0.91
	11	−1.29	0.95

Short song bout = 10 phrases, medium song bout = 19 phrases and long song bout = 30 phrases.

(with the exception of individual 3) had the lowest slope between H1 and H2. All of these analyses indicate that the spectacled warbler's song follows a first-order Markov chain, that is, the utterance of each syllable depends only on the previous syllable uttered (Fig. 3; Appendix Fig. A2), and that there were no differences between groups.

Versatility

Syllable and pair versatility were very similar among the three groups, and in both cases the values were close to 0.6 (Appendix Table A3), which indicates that 60% of the syllables in one phrase were different and the same percentage of pairs (sequences of two syllables) uttered were built by different syllables. The ANOVA did not show any significant differences between song bout groups ($F_{2,15} = 1.40$, $P = 0.276$ for syllable versatility and $F_{2,15} = 1.49$, $P = 0.26$ for pair versatility). There was no correlation between versatility and repertoire size in any of the song bout groups (these results show syllable versatility and pair versatility versus repertoire size, respectively: short song bout: $r_2 = -0.32$, $P = 0.68$; $r_2 = -0.01$, $P = 0.98$; medium short bout: $r_8 = -0.16$, $P = 0.64$;

Table 2
Overview of information associated with sampled individuals

Individual	Phrases	Syllables/phrase	Total syllables	Locality	Zone	X	Y
1	19	14.9	284	Barranco Esquinzo	28R	568 388.67	3 105 590.50
2	19	13.5	256	Huertas Chilegua	28R	579 715.00	3 125 678.00
3	30	24.1	723	Antigua	28R	594 708.10	3 143 690.51
4	19	14.1	267	Betancuria	28R	592 082.00	3 142 238.00
5	19	15.6	297	Betancuria	28R	591 933.43	3 142 901.63
6	29	20.2	585	Guisguey	28R	609 061.00	3 159 999.00
7	19	21.3	404	Guisguey	28R	609 150.94	3 159 927.68
8	30	14.1	424	Malpaís de la Arena	28R	605 350.93	3 166 659.98
9	19	20.9	398	Majanicho	28R	604 374.53	3 174 616.38
10	19	18.4	350	Vallebrón	28R	609 826.53	3 162 466.24
11	30	19.7	590	Barranco Los Canarios	28R	569 572.00	3 109 181.00
12	19	20.9	397	Guisguey	28R	608 974.70	3 159 826.83
13	19	18.2	345	Guisguey	28R	608 769.08	3 159 859.54
14	19	16.6	316	Tetir	28R	603 819.51	3 155 235.03
15	10	15.7	157	Barranco Esquinzo	28R	568 537.24	3 104 926.87
16	10	22.5	225	Barranco Los Canarios	28R	569 572.00	3 109 252.32
17	10	23.0	230	Antigua	28R	594 383.00	3 143 645.00
18	10	19.6	196	Guisguey	28R	609 150.94	3 159 927.68

List of individuals recorded with information on the number of phrases uttered, mean number of syllables by phrase, total number of syllables analysed, locality where it was recorded and coordinates according to the UTM format.

Figure 2. Examples of Zipf's graphs, in which the logarithm in base 10 of the frequency of the syllable uttered by individuals is plotted (from the commonest to the rarest) (LogUttered) against the logarithm of its rank of use per individual (first, second, third, etc. syllable; LogRank). Regression equations are also shown, along with the squared regression coefficient. (a) An individual with a short song bout; (b) an individual with a medium song bout; (c) an individual with a long song bout.

Table 4
Overview of results of parameters quantified

Information value	Short song bout (20.2 syllables/phrase)	Medium song bout (17.4 syllables/phrase)	Long song bout (19.5 syllables/phrase)
H0	5.34±0.24	5.62±0.35	5.92±0.13
H1	3.97±0.22	4.04±0.34	3.86±0.49
H2	1.46±0.11	1.72±0.19	1.84±0.13
H3	0.87±0.17	0.98±0.06	1.20±0.12
H4	0.61±0.13	0.69±0.08	0.85±0.14
H5	0.41±0.08	0.46±0.13	0.59±0.15
H6	0.28±0.04	0.27±0.11	0.43±0.11
RE1	0.75±0.07	0.72±0.05	0.65±0.07
RE2	0.27±0.01	0.31±0.03	0.31±0.02
RE3	0.16±0.03	0.18±0.02	0.20±0.02
RE4	0.11±0.02	0.12±0.02	0.14±0.03
RE5	0.08±0.01	0.08±0.03	0.10±0.03
RE6	0.05±0.01	0.05±0.02	0.07±0.02
RD1	0.25±0.07	0.28±0.05	0.35±0.07
RD2	0.73±0.01	0.69±0.03	0.69±0.02
RD3	0.84±0.03	0.82±0.02	0.80±0.02
RD4	0.89±0.03	0.82±0.02	0.86±0.03
RD5	0.92±0.01	0.92±0.03	0.90±0.02
RD6	0.95±0.01	0.95±0.02	0.93±0.02
ObsRep	41±6.58	50.4±11.94	60.75±5.44

Values of mean entropy orders (H), mean relative entropy (RE), mean redundancy (RD) and observed repertoire (ObsRep) are shown with their respective standard deviations per group of song bout duration (short song bout = 10 phrases, medium song bout = 19 phrases and long song bout = 30 phrases).
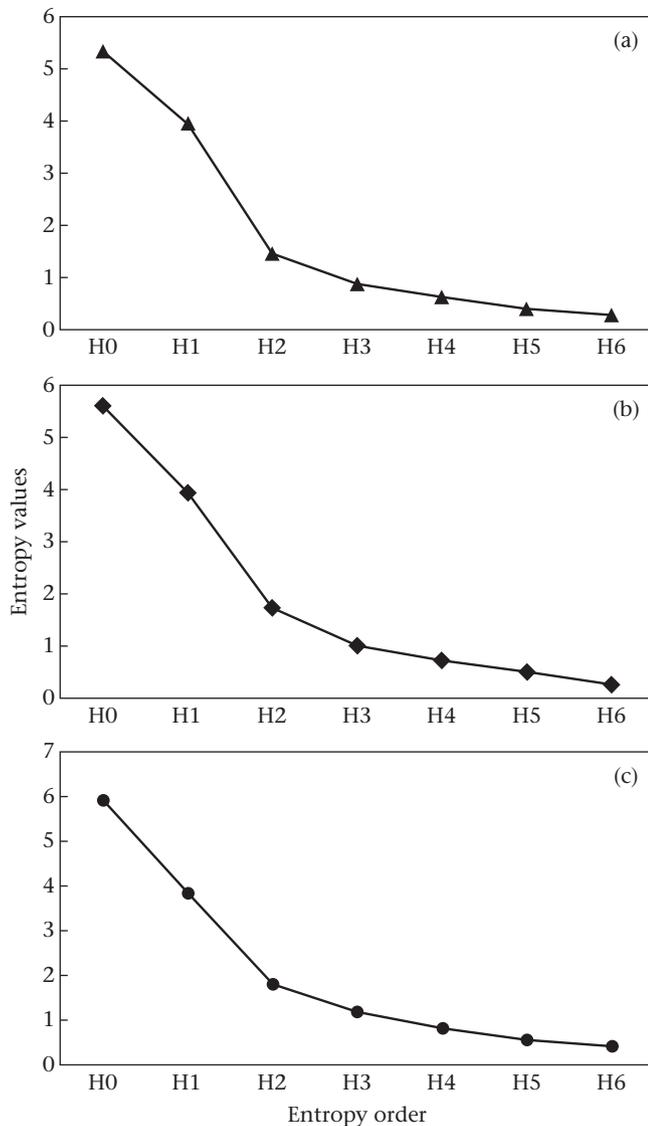
like syllable. However, in the analysed set of 10 pairs most frequently uttered, we observed that between 10 and 80% of these most frequent pairs were not shared among individuals (Fig. 4), such that the most frequently uttered pairs per individual were different for each. We then looked for these pairs in the entire repertoire of pairs uttered by individuals, to assess whether they were uttered by all individuals but with different frequency of occurrence. We found that the number of these sets of pairs that were uttered by only one individual varied from 0 to 100% (Fig. 4); some of them were shared but most were just uttered by one individual.

These results suggest that the degree of individual exclusivity in generating particular pair types is fairly high (despite the fact that they shared several pairs, the frequency of utterance was very different between individuals).

DISCUSSION

Song Complexity Versus Song Duration

Song complexity may be a costly sexual character under strong selection (Catchpole & Slater, 2008; Nowicki et al., 2000; Nowicki, Peters, & Podos, 1998; Searcy & Andersson, 1986), and thus detailed information on internal organization of songs could aid in the understanding of the targets of sexual selection and whether trade-offs exist between song features. Our results show that spectacled warbler songs, despite being of variable length, presented no significant differences in structure complexity, as quantified by entropy orders, Markov chaining, versatility and Zipf's law. Individual warblers varied their song length to a great extent but shifts were not associated with changes in complexity of the internal structure of the song. This suggests that the prediction that song bout length should be positively related to the complexity of individual songs (because only high-quality individuals can afford the costs of both features, Chappell et al., 1995; Eberhardt, 1994; Nowicki & Searcy, 2005) is not supported. However, the

$r_8 = -0.49$, $P = 0.15$; long song bout: $r_2 = 0.90$, $P = 0.09$; $r_2 = 0.91$, $P = 0.08$; all together: $r_{16} = -0.27$, $P = 0.26$; $r_{16} = -0.27$, $P = 0.27$).

Song Sharing

We found a lack of correlation between the geographical distance and individuals' syllable sharing ($r = -0.26$, $P = 0.89$) and pair sharing ($r = 0.04$, $P = 0.39$).

Only four syllables were shared by all individuals recorded, one of them being the starting syllable (at the beginning of the phrase), and another presenting a trill-like structure (Fig. 1). The pair types composed of a repetition of the same syllable constituted 3.45–11.5% of the total repertoire of pairs uttered per individual. In these same-syllable pairs, the percentage of exclusivity (pair types uttered by only one individual) varied from 0 to 57.14% with an average ± SD of 28.50 ± 14.32. When we compared the 10 most frequent pairs uttered by each individual, we found that the same pair appeared to be the most frequent among all individuals, and that this specific sequence was formed by a repetition of the trill-

Figure 3. Information graph of the mean entropy values for each entropy order of the following groups: (a) short song bouts; (b) medium song bouts; (c) long song bouts.

Collins, De Kort, Pérez-Tris, & Tellería, 2009; Feßl & Hoi, 2000; Szekely, Catchpole, Devoogd, Marchl, & Devoogd, 1996). The different combinations of syllables created by each individual might be acting as an informative trait that helps in the mate selection process, and some specific syllables or combination thereof may have a more important functional meaning than the repertoire per se (see below). Podos, Peters, Tamia, Marler, and Stephen (1992, pp. 100–101) noted that 'a repertoire of highly dissimilar songtypes might be functionally different from a repertoire of the same size but with more similar songtypes', suggesting that the internal structure of the song is likely to be important and should be studied while addressing female selection or male–male competition.
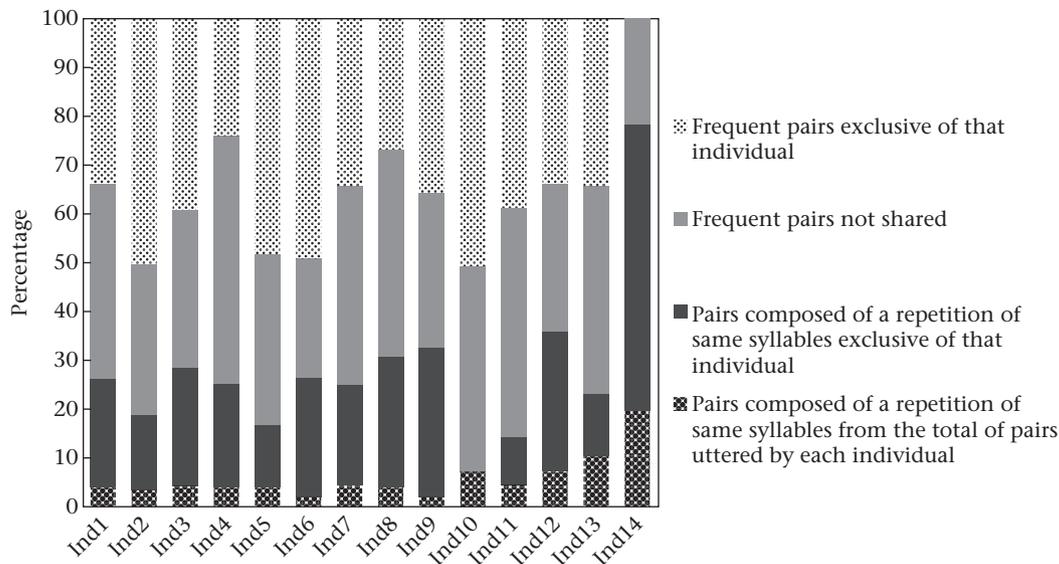
Zipf's Statistic and its Implications

The song of the spectacled warbler presented an 'appropriated' communication system according to the characteristics recorded in Zipf's law, that is, it is neither too repetitive nor too diverse, is in a state of optimal balance (Doyle, McCowan, Johnston, & Hanser, 2011; McCowan, Doyle, Jenkins, & Hanser, 2005) and possesses a capacity to transmit information similar to that of human languages when excluding the metacommunication and dialogue aspects typical of our spoken languages (Doupe & Kuhl, 1999; McCowan et al., 1999). As expected in those species that use vocal communication as a primary mode of social interaction, spectacled warblers showed a Zipf's statistic close to −1 in all the individuals analysed regardless of the song bout length, presenting a high potential for communication capacity (McCowan et al., 1999). Eight individuals showed values below the Zipf's statistic (from −1.22 to −1.43), which suggests that they had slightly more redundant repertoires and lower potential communication capacity. Previous studies have shown that young individuals that learn vocal communication at early developmental stages usually present lower values of Zipf's slope than conspecific adults (McCowan et al., 1999; McCowan & Reiss, 1995a, 1995b). We have no data on the age of the recorded individuals, although we assume that there were no large age-related differences in our sample since all recorded birds were territorial adult males, and warbler species are typically very short-lived (Payevsky, 1999; Shirihai, Gargallo, Helbig, Harris, & Cottridge, 2001). Therefore, our results indicate that variation in the Zipf's statistic within a population does exist, and that the causal mechanisms of this pattern need to be investigated further in this species.

Finally, Zipf's graphs also suggest that spectacled warbler communication might be an open system (new syllables are encountered when sample size increases), since the left part of the graph did not adjust a zero asymptotic slope (Ficken, Hailman, & Hailman, 1994; Hailman et al., 1985). That generative property is considered fundamental in language definition (Diebold, 1968), and has been previously documented in black-capped chickadees, *Parus atricapillus* (Hailman et al., 1985) and Mexican chickadees, *Parus sclateri* (Ficken et al., 1994).

Shannon Theory and Markov Chaining

We found that the spectacled warbler's song possesses a certain internal structure as highlighted by the entropy measures. A loss of information was observed between the first and the second order of entropy, indicating that male song follows a first-order Markov chain. This indicates that the information decreases at the level of sequences of two syllables and therefore each syllable is highly dependent on the previous one (Briefer et al., 2010; Gentner & Hulse, 1998; Lemon & Chatfield, 1973), implying that the formation of sequences of two syllables was more predictable. This may be caused by some mechanical or biological constraints while the

alternative prediction that song complexity should be negatively related to duration (trade-off hypothesis, Gil & Gahr, 2002; Soma, Takahasi, Hasegawa, & Okanoya, 2006) is also unsupported, since no significant negative relationships resulted between these features. Although the relative increment of information was very similar in all the song bout groups as highlighted by Shannon theory and Markov chaining, we did observe that some higher entropy order values differed significantly between groups. These differences, however, are due to the different syllable repertoire sizes of each individual and group, since H0 is closely related to repertoire size, and the different numbers of sequences in song bouts of different lengths mean that one long song bout will have more sequences of at least five syllables than short or medium song bouts.

The lack of differences in internal complexity between song bouts should be investigated by additional studies in this species, to detect whether singing a variable song is more costly than singing a stereotypic song bout, or whether a high degree of song complexity is inherent to the communication system of the species (species of the Sylviidae group have complex repertoires; Catchpole, 1976;

Figure 4. Bar graphs representing the percentages of exclusivity according to the type of pairs: pairs composed of a repetition of the same syllable from the total of pairs uttered by each individual, pairs composed of a repetition of the same syllable exclusive of that individual, the 10 most frequent pairs that are not shared, and frequent pairs exclusive of an individual (considering all the pairs uttered by an individual).

remaining sequences composed of more syllables are not affected and are created with greater freedom of choice, as proposed by Briefer et al. (2010) for the skylark. Compared with other species, syllable repertoire diversity (H0 = 5.64 ± 0.31 SD) and simple repertoire internal organization (H1 = 3.92 ± 0.49 SD) were similar to values found in higher vertebrate groups such as in the chucks of squirrel monkeys (H0 = 2.81 and H1 = 2.21, McCowan et al., 2002) and the whistles of bottlenose dolphins (H0 = 4.75 and H1 = 1.92, McCowan et al., 2002). Compared to those of other oscines previously studied, entropy order values for spectacled warblers appear to be similar to or higher than those of the hermit thrush, *Hylocichla guttata* (H1 = 3.4, Dobson & Lemon, 1978), the wood thrush, *Catharus mustelina* (H1 = 3.5–4.5, Dobson & Lemon, 1978), the American robin, *Turdus migratorius* (H1 = 3.5–4, Dobson & Lemon, 1978), the veery, *Hylocichla fuscescens* (H1 = 2, Dobson & Lemon, 1978), the European starling, *Sturnus vulgaris* (H0 = 7 and H1 = 6, Gentner & Hulse, 1998), the rufous-bellied thrush, *Turdus rufiventris* (H1 = 3.19, Da Silva et al., 2000) and the skylark (H0 = 7.4 and H1 = 7.0, Briefer et al., 2010). The skylark and the European starling are the only studied species to date that have presented higher values of entropy, and therefore the spectacled warbler could be considered among the species with a high level of internal song complexity.

Besides entropy order values, we analysed transition versatility and observed that both syllable transitions and pair transitions reached a mean value of 60%, being highly versatile (Ince & Slater, 1985). In keeping with Hartshorne (1956), this result indicates that the spectacled warbler could be varying its song to avoid habituation in the receiver, since this is also combined with a high degree of syllable and pair transition (Ince & Slater, 1985; Leger, Brooks, & O'Brien, 2000; Nowicki, Peters, Searcy, & Clayton, 1999). Although we did not study frequency shifting, these modifications suggest that the species creates variation during a song bout (Leger et al., 2000).

Song Sharing among Individuals

Contrary to our expectations, individuals did not show a pattern of song sharing as a function of geographical distance, and thus close neighbours did not share more syllables or pairs than distant individuals. This is not in line with previous analyses in which a geographical correlation was found (Briefer et al., 2010; Franco & Slabbekoorn, 2009; Laiolo & Tella, 2006; Rivera-Gutiérrez, Matthysen, Adriaensen, & Slabbekoorn, 2010). In some cases song sharing between neighbours was related to territory maintenance (Beecher, Campbell, Burt, Hill, & Nordby, 2000; Wilson, Towner, & Vehrencamp, 2000), facilitating a decrease in aggressive interactions between neighbours (Baker, Thompson, Sherman, & Cunningham, 1981), and possibly depending on the degree of isolation of males on the mainland (Laiolo & Tella, 2005) or on islands (Lachlan & Slater, 2003; Morton, 1987). Our study focused on one island without conspicuous geographical barriers, and on a species with good dispersal capabilities owing to its migratory habits in large parts of its distribution (Cramp, 1992). Fuerteventura lacks major topographical or habitat barriers for the species, and individuals may therefore move freely throughout the island. Consequently, if we also consider that sometimes the isolation of populations (considering a population as the island) may cause an increase in song variation (Osiejuk, Ratyńska, Cygan, & Dale, 2003), the expected outcome would be no relationship between geographical distance and song sharing. Our results support a previous study where no correlation was found between differentiation in spectrotemporal features and geographical distance in this species (Palmero et al., 2012), suggesting that the low spatial organization of songs is possibly due to the lack of habitat barriers on the island. Birds frequently learn their songs by imitating their neighbours (Hultsch & Todt, 2004; Lachlan & Servedio, 2004; Slater, 1986), but in our study it is not clear how spectacled warbler individuals learn their repertoire without sharing it with their neighbours, as in the case of the rufous-bellied thrush (Da Silva et al., 2000). One possibility is that individuals are learning different syllables or syntactical structures from different individuals during their dispersal phase, creating a great variability within an area, as in the common chaffinch, *Fringilla coelebs* (Slater, 1986). In addition, the spectacled warbler is short-lived and individuals probably lack long-term neighbours, and thus there is likely to be no advantage in maintaining the levels of song sharing among neighbours typical of species with high territorial fidelity (Beecher & Brenowitz, 2005;

Koetz, Westcott, & Congdon, 2007; Kroodsma, 1996; Lachlan & Servedio, 2004; Wilson & Vehrencamp, 2001).

The four syllables that were shared among all individuals may reflect intrinsic features of the species, important for species recognition or with some functional relevance. One of these syllables, the trill-like syllable, was the most frequent syllable and pair (two equal syllables) in all individuals. It has been proposed that uttering these trilled structures is costly (Doutrelant, Blondel, Perret, & Lambrechts, 2000; Oberweger & Goller, 2001) and may reveal male quality (Cramer, 2013; Galeotti, Saino, Sacchi, & Møller, 1997; Garamszegi, 2005; Laiolo et al., 2004). In addition, they may play a role in male competition and territory defence (Galeotti et al., 1997; Trillo & Vehrencamp, 2005), an idea that is supported by the fact that the spectacled warbler utters a similar syllable in alarm and warning calls (Cramp, 1992).

Conclusions

The spectacled warbler possesses a complex and highly variable song that follows a first-order Markov chain comparable to vocalizations in other higher social vertebrates and that shows generative properties. Our results do not present significant correlations between song length and internal complexity, but rather high levels of versatility in all the groups. There was no pattern of song sharing as a function of geographical distance, and this pattern may be responsible for the great variability of songs within an area. This study shows the great potential of information theory applied to animal communication systems, and the number of characteristics that can be assessed by this method, with implications for the development and the evolution of animal communication.

Acknowledgments

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Appendix

Table A1

Differences in entropy orders between song bout groups assessed with *t* tests

| Entropy order	Short versus Medium	Medium versus Long	Short versus Long
H0	$t_{12}=-1.43$, $P=0.18$	$t_{12}=-1.65$, $P=0.13$	$t_{6}=-4.26$, $P=0.01$
H1	$t_{12}=0.38$, $P=0.71$	$t_{12}=0.81$, $P=0.43$	$t_{6}=0.42$, $P=0.69$
H2	$t_{12}=-2.62$, $P=0.02$	$t_{12}=-1.08$, $P=0.29$	$t_{6}=-4.36$, $P=0.01$
H3	$t_{12}=-1.27$, $P=0.29$	$t_{12}=-3.55$, $P=0.03$	$t_{6}=-3.19$, $P=0.02$
H4	$t_{12}=-1.34$, $P=0.21$	$t_{12}=-2.83$, $P=0.15$	$t_{6}=-2.48$, $P=0.05$
H5	$t_{12}=0.78$, $P=0.45$	$t_{12}=-1.57$, $P=0.14$	$t_{6}=-2.09$, $P=0.08$
H6	$t_{12}=0.26$, $P=0.80$	$t_{12}=-2.43$, $P=0.03$	$t_{6}=-2.56$, $P=0.04$

Table A2

Slope variation among the entropy order transitions and between song bout groups

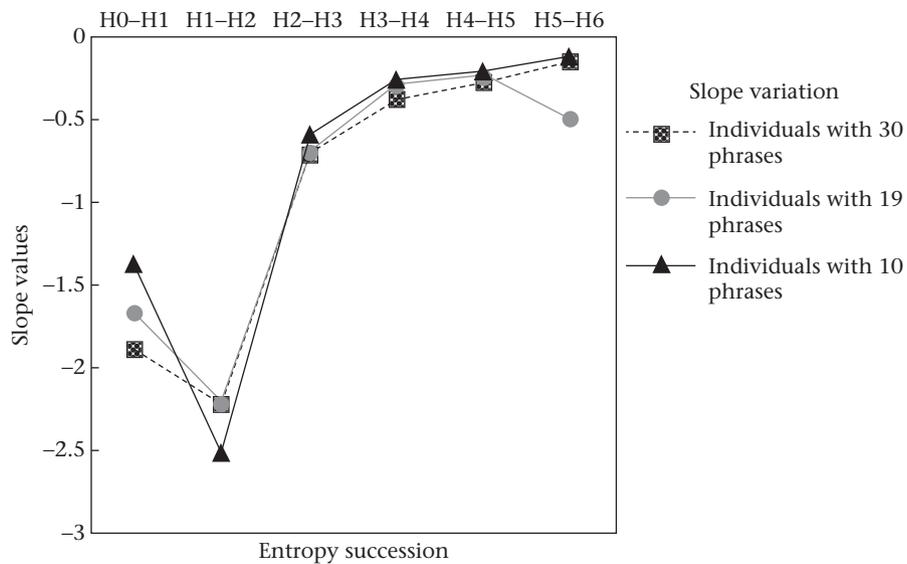| Slope variation	Short song bout	Medium song bout	Long song bout	Long song bout without individual 3
H0-H1	−1.37	−1.67	−2.06	−1.88
H1-H2	−2.51	−2.22	−2.02	−2.22
H2-H3	−0.59	−0.69	−0.64	−0.71
H3-H4	−0.25	−0.29	−0.35	−0.37
H4-H5	−0.21	−0.23	−0.26	−0.27
H5-H6	−0.12	−0.49	−0.16	−0.15

We considered short, medium and long song bouts, and added another group that represents the data of individuals with a long song bout after removing one atypical individual (individual 3).

Table A3

Mean ± SD syllable versatility and pair versatility per song bout group

	Short song bout	Medium song bout	Long song bout
	$N=4$	$N=10$	$N=4$
Syllable versatility	0.60±0.09	0.56±0.06	0.52±0.06
Pair versatility	0.61±0.06	0.63±0.06	0.60±0.07
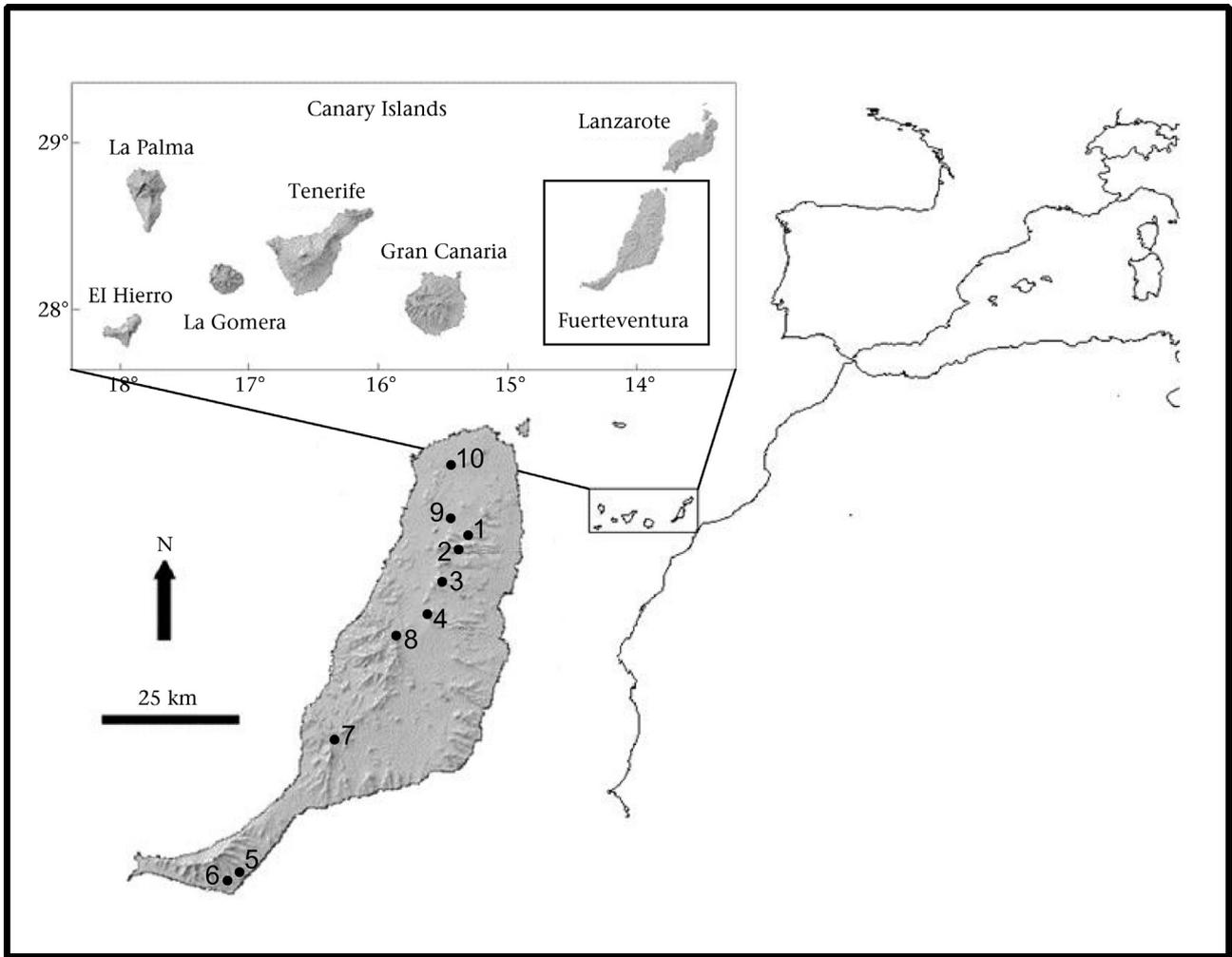
Figure A1. Map of Fuerteventura. The centroids obtained from the position of individuals recorded in the different localities are indicated. 1: Vallebrón, 2: Guisguey, 3: Tetir, 4: Antigua, 5: Barranco Los Canarios, 6: Barranco de Esquinzo, 7: Barranco de Chilegua, 8: Betancuria, 9: Malpaís de la Arena, 10: Majanicho.

Figure A2. Representation of the slope of the mean entropy values of the three song bouts: short, medium and long (long song bouts exclude the atypical individual 3). Short song bout = 10 phrases, medium song bout = 19 phrases and long song bout = 30 phrases.