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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.

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 grosbeaks, *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 repertoires 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 signals with a simple internal structure or short and complex ones in order to achieve a cost–benefit balance. Alternatively, since birdsong 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 hypotheses, 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 individuals 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 syllables 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).

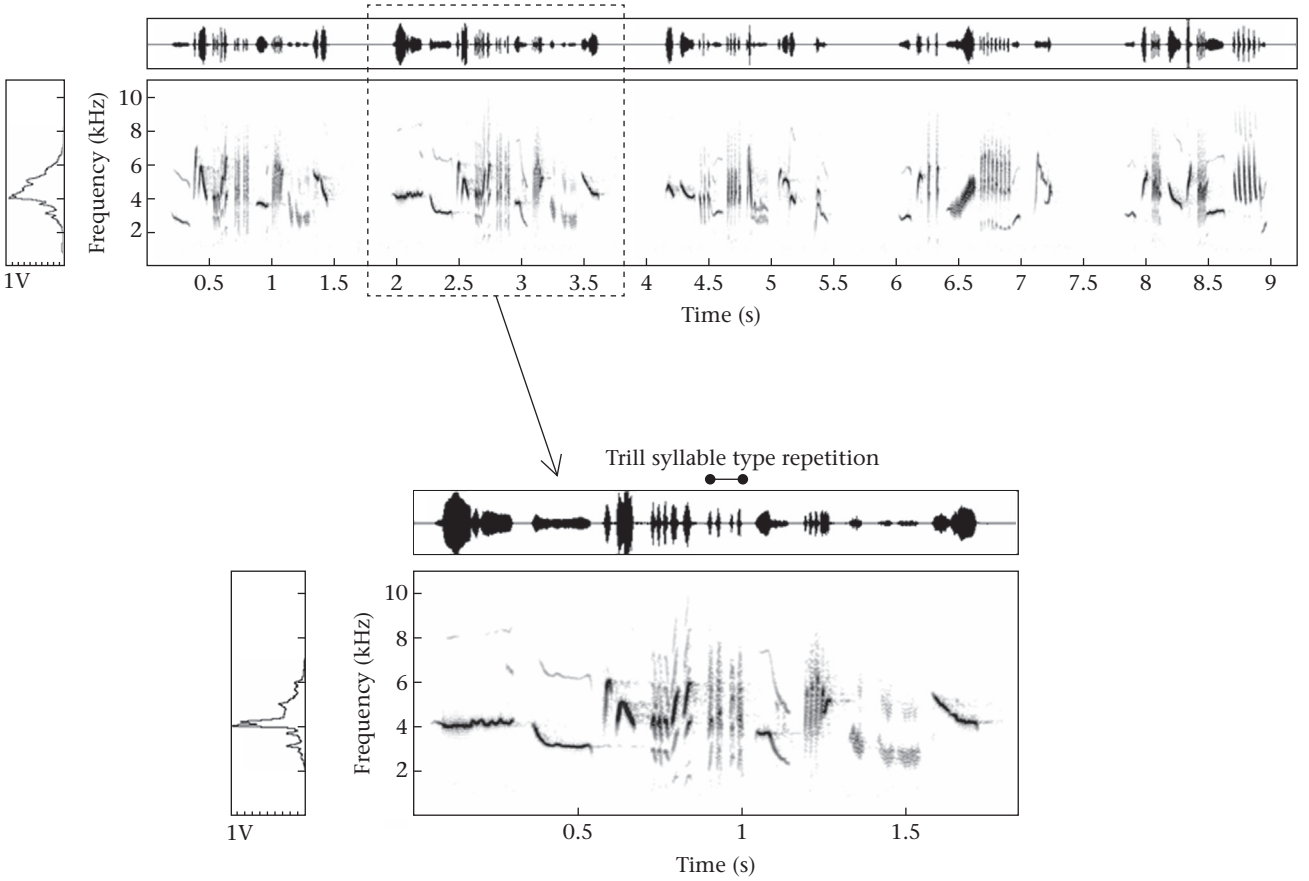

Figure 1. Portion of a song bout of a spectacled warbler male from Fuerteventura island. The interphrase time has been reduced to allow five consecutive phrases to be shown. A detail of one phrase with a trill syllable type repetition in the middle of the phrase is also shown.