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The two parts of the blackcap song: Acoustic analysis and male responses to playbacks

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ABSTRACT

Bird songs are complex manifold acoustic signals serving two main functions: mate attraction and territorial defense. The way information is encoded in the song often reflects adaptation to proximate and ultimate constraints. Male blackcaps, *Sylvia atricapilla*, display versatile songs with two parts, a warble and a whistle, whose functions remain unclear. We showed that the two parts of songs differ in terms of intensity, frequency and temporal parameters. They also contain totally different sets of syllables. Furthermore, the warble is versatile whereas the whistle part shows syllable sharing between individuals leaving closeby. Altogether, the results of our analysis suggest that the two parts encode different information potentially directed to different audiences. In order to test the potential function of these two parts, we performed playback experiments by broadcasting entire songs and each part separately. Warble and whistle alone are sufficient to trigger male responses and males sing both parts in responses to all stimuli, showing that both parts of the song are used in male–male competition. It is suggested that the segregation of information in the blackcap song could be related to public versus private communication, used in both intra- and intersexual contexts, rather than directed to male versus female audiences only.

1. Introduction

Songbirds, psittaciforms and hummingbirds are the three known groups of birds producing vocalizations which are learned from conspecifics. Learned songs are known to have two main functions: territorial defense and mate attraction (Marler and Slabbekoorn, 2004). To fulfill efficiently its two main functions, birdsongs must often encode different information such as species identity, group label, individual identity, physical quality and motivational state (Catchpole and Slater, 2008). This information can be encoded at the same place in the song. For example, in the white-throated sparrows, *Zonotrichia albicollis,* and the field sparrows, *Spizella pusilla*, song frequency seems to be used both for species and individual identity (Brooks and Falls, 1975; Nelson, 1989). But conflicts between different information may exist. For example, group label or species identity and individual identity are antagonist because the first ones imply sharing (or similarity) and the second one implies distinction (or dissimilarity). One way of resolving the conflict can be the segregation of information. In the white-crowned sparrow, *Zonotrichia leucophrys*, the individual identity is encoded into a particular note ("the complex note") while the dialect identity is encoded into the trill phrases (Nelson and Poesel, 2007). Another way of resolving the conflict may be to select which audience information should reach. The information can be either public, when the sender advertises and transmits information to a wide audience, or private, when the active space of the signal is limited to a restricted number of receivers (Dabelsteen and McGregor, 1996; McGregor, 2005). If the information is public, it has to be resistant to degradation to be heard by many individuals. On the contrary, if it is a private information, it could be advantageous that the signal does not propagate at long range. For example, in the white-browed warbler, *Basileuterus leucoblepharus*, the species-specific information is encoded in a resistant acoustic feature (slow descending modulation frequency) while the individual identity is supported by song features susceptible to degradation (the frequency gap of the higher pitched part) (Mathevon et al., 2008).

The blackcap (*Sylvia atricapilla*), is a small passerine breeding in western Palearctic and wintering in southern Europe and Africa (Wesołowski, 2011). During the breeding season, males settle in forest edges and parklands, in adjacent and stable territories which they defend actively. Males display songs of 3–7 s with 2 parts which can be easily distinguished by ear. In several studies (Collins

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et al., 2009; Sauer, 1955), it has been suggested that the warble part could be a signal bearing information directed to females and the whistle part a signal directed to males. Indeed, authors observed, that the warble is longer when females are fertile and used more frequently in extrapair copulation context. On the other hand, the whistle becomes either shorter and more stereotyped (Sauer, 1955) or longer (Leedale et al., 2015) during male–male aggression. However, as point out by Byers (Byers, 2011) there is still no good evidence concerning separate functions of the two parts of the blackcap song. Thus, the song of the blackcap provides an interesting model to study the relationships between intra- and intersexual selection pressures as well as how different information can be encoded in a song.

In this study, we performed a detailed acoustic and syntactical analysis of the blackcap's song. We hypothesize that if the two song parts bear distinct information, those parts could show different acoustic characteristics. We also performed playback experiments to test the behavioral responses and the singing responses of males challenged with the warble part alone, the whistle part alone or the entire song.

2. Materials and methods

2.1. Ethical note

This study was performed under proper legislation of the French law and was approved by the Ethical Committee of Paris Center and Sud.

2.2. Study area, subjects and song recordings

This study was carried out in France during the breeding season, from March to July 2013. 28 males established in 5 different locations (4–10 males per group) were recorded in the campus of the University of Paris-Sud and in Corsica Island (Saint Florent, Evisa). We recorded individuals between 0600 and 1200 h Eastern Daylight Time using a Marantz PMD 661 numeric recorder (sampling rate: 44.1 kHz) connected to a Sennheiser MKH70 directional microphone (frequency response: 50 Hz–20 kHz ± 1 dB). In order to follow and recognize individuals on several days of recordings, each male adult tested was first captured in mist nets and ringed with a unique combination of three plastic color rings. We took the GPS coordinates of each male to locate the individual territory boundaries.

2.3. Song analysis

For song analyses, we used Avisoft SASLab pro v.5.2.07 software and Sound Analysis Pro v2011.104 (Tchernichovski et al., 2000). Song files were first high-pass filtered (FFT filtering, cut-off frequency: 1600 Hz) to remove the low-frequency background noise. Then, we selected ten songs per individual with the highest signal to noise ratio. Songs were analyzed on a sound spectrogram (FFT-length: 1024; Frame: 100%; Hamming window, Fig. 1). A syllable was defined as a continuous trace on the sound spectrogram or a group of continuous traces spaced out by less than 25 ms.

On the basis of their frequency modulation shapes, we classified all the syllables for 6 individuals. Repertoire sharing (RS) of syllables were calculated as follows: $RS = Z/((X+Y)-Z)$, with X and Y being the total number of syllables produced by males X and Y, and Z being the number of syllables shared by males X and Y (Hultsch and Todt, 1981). RS values range from 0 to 1, with 1 being maximum sharing. We calculated the relative complexity of the two parts as the ratio between the number of different syllables and total number of syllables in the corresponding part.

In order to characterize acoustic parameters, each syllable was first analyzed separately and we then calculated an average for all syllables produced. We measured the following five frequency parameters: the frequency of maximum amplitude (peak frequency, measured on the mean spectrum of the entire syllable), the frequency values at the upper limit of the first (25%), second (50%) and third (75%) quartiles of energy, the minimum frequency and the bandwidth (difference between maximum frequency and minimum frequency). As temporal parameters, we measured the duration of syllables (duration), the duration of gaps between two successive syllables (gap) and the duration of each syllable plus the successive gap (interval). We then used the temporal parameters to calculate the rhythm (ratio sound versus silence) and the tempo (number of syllable by second). We also measured the Wiener entropy, which estimates the width and uniformity of the power spectrum. Finally, we calculated the ratio between the amplitude of the warble part versus the amplitude of the whistle to obtain the relative amplitude of each part.

For all statistical tests, we used R v2.13.0. All means are given ±SE. We used general linear model to compare the differences in acoustic parameters between the two parts of the song with part of the song included as fixed factor and subject as random. We used the Wilcoxon matched pairs signed-rank test (data were not normally distributed) to compare the differences for entropy and song complexity between the two parts of the song. We performed an exact paired permutation test using Monte Carlo method to compare the repertoire sharing.

2.4. Playback experiments: subjects and stimuli

We carried out playback experiments in the fields surrounding the University of Paris Sud, in June 2014 when blackcaps defend their territory against intruders. The playback experiments were conducted between 0600 and 1200 h on 12 males paired with a female. As for many songbirds, songs are sung in bouts mainly during the dawn chorus and again at the end of the afternoon (pers. obs, Mason, 1995). We created stimuli using blackcap's songs from

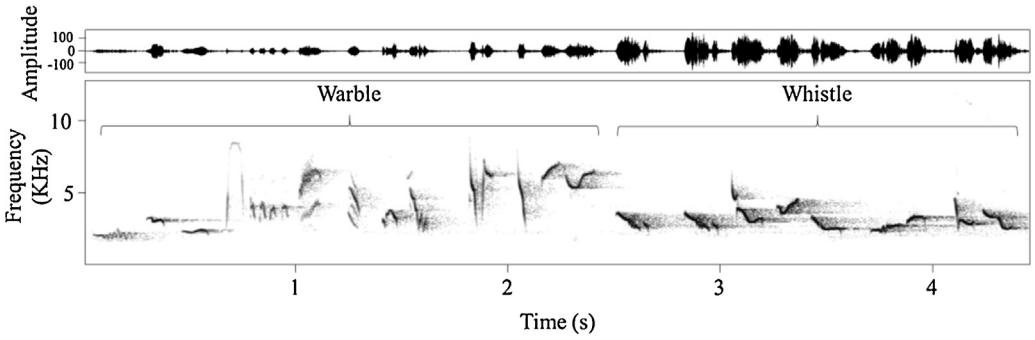

Fig. 1. Oscillogram(above) and spectogram (below) blackcap's song.