ELSEVIER

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



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



Juliette Linossier^{a,b,*}, Hélène Courvoisier^{a,b}, Thierry Aubin^{a,b}

- ^a Université Paris-Sud, Institut de NeuroScience Paris Saclay (NeuroPSI), UMR 9197, Orsay, France
- ^b CNRS, Orsay, France

ARTICLE INFO

Article history:
Received 25 April 2015
Received in revised form 1 October 2015
Accepted 10 October 2015
Available online 30 October 2015

Keywords: Blackcap Sylvia atricapilla Birdsong Acoustic analysis Playback Information Audience

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.

© 2015 Elsevier B.V. All rights reserved.

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

^{*} Corresponding author at: Université Paris-Sud, Institut de NeuroScience Paris Saclay (NeuroPSI), UMR 9197, Orsay F-91405, France. Fax: +33 168157726. E-mail address: juliette.linossier@u-psud.fr (J. Linossier).

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: $50\,\mathrm{Hz}{-}20\,\mathrm{kHz}{\pm}1\,\mathrm{dB}$). 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 Y being the number of syllables shared by males Y 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 \pm 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

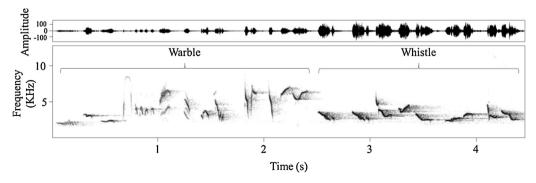


Fig. 1. Oscillogram(above) and spectogram (below) blackcap's song.

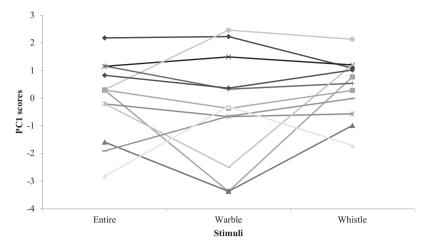


Fig. 2. Individual PCI scores (N = 12) in response to the three broadcasted stimuli.

the Corsican population in order to prevent any potential dearenemy effect that could reduce territorial response. To build the stimuli, we used 12 different songs from 10 different males to avoid pseudo replication. Each bird received a set of 3 stimuli: the warble part alone, the whistle part alone and the entire song. Each stimulus consisted of songs separated by 2.5-4.5 s of silence to mimic the natural rate, and was played back for 90 s. We rescaled each song part to root mean square equalized amplitudes using a script implemented in Praat (www.gbeckers.nl/pages/praat_scripts/rms_ equalize.praat_script). We broadcasted songs with a FoxproFury GX7 remote-controlled autonomous amplifier at the intensity estimated to be normal for the bird (78 dB for warble and 85 dB for whistle, Mathevon and Dabelsteen, 2002). The loudspeaker was positioned close to the ground, in a tree grove when possible, within the subject's territory. The playback session was initiated when the subject was inside its territory at more than 10 m from the loudspeaker. The order in which the 3 stimuli were presented was balanced and presentations of stimuli were separated by at least 10 min to ensure that birds recover a normal activity between playbacks. For each stimulus, the response of the subject was observed during 180s, corresponding to the broadcast of 90s of song and 90 s of post-playback silence. Blackcaps display a strong territorial behavior with stereotyped patterns, which are easy to observe. A male reacts vigorously against territorial intrusion by flying toward the intruder and by landing in its vicinity or flying around it. It also produces songs and calls toward the intruder. We measured the latency before the first song, the number of songs produced during the playback experiment, the latency before the first approach toward the loudspeaker and the time spent between 0 and 5 m, between 5 and 10 m and at more than 10 m from the loudspeaker

(Table 3). At the same time, we recorded the songs produced by the focal males during and after the playback experiment.

We first used a Friedman two way ANOVA test to compare the territorial response to the different stimuli. Second, we used a principal component analysis (PCA) after examination of the correlation matrix to create composite scores reflecting the intensity of responses observed during the playback experiment. No variables were highly correlated (Pearson correlation <0.5). We then compared the responses to the different stimuli using an ANOVA test. The dependent variables were the PCA scores and the order of stimulus presentation whereas the type of stimulus (S1, S2 and S3) was the independent variables. Subject identity was included as a random factor.

3. Results

3.1. Acoustics characteristics of the two parts

The amplitude of the whistle is three times higher than the amplitude of the warble (3.1 \pm 0.089). Moreover all the other acoustics parameters measured, except part duration, are significantly different between these two parts (Table 1).

The warble has a higher peak frequency, higher quartiles values, lower minimum and higher maximum frequencies with a broader bandwidth and a lower rhythm compared to the whistle.

Among all the 280 songs analyzed, the warble was more often missing than the whistle (99.9% of songs contain the whistle while 84% contain the warble).

Table 1 Comparison of the acoustic characteristics of warble and whistle parts (mean \pm SE, n = 28 subjects).

Acoustics parameters	Warble	Whistle	GLM (Df = 1)	
			\overline{F}	<i>P</i> -value
Peak frequency (Hz)	4036 ± 28.9	3277.4 ± 12.7	174.5	>0.001
Bandwidth (Hz)	556 ± 8.6	463.8 ± 6.1	40.7	>0.001
Quart 25 (Hz)	3534.4 ± 23.3	3079.1 ± 10.2	76.9	>0.001
Quart 50 (Hz)	4182.1 ± 27.5	3335.6 ± 12	266.7	>0.001
Quart 75 (Hz)	4990.7 ± 36.9	3630.6 ± 16.8	365.5	>0.001
Rhythm	1.02 ± 0.017	1.5 ± 0.02	197.5	>0.001
Minimum frequency (Hz)	2247 ± 29.2	2704.3 ± 10.4	57.4	>0.001
Maximum frequency (Hz)	6039.8 ± 65.9	3949.5 ± 20.3	250.8	>0.001
Part duration (s)	2.34 ± 0.09	2 ± 0.06	0.8	0.37
Syllable duration (s)	0.07 ± 0.001	0.096 ± 0.001	108.4	>0.001
Tempo	6.9 ± 0.09	6.2 ± 0.06	12.8	0.0012

Table 2 Measures of the territorial responses recorded during playback experiments toward the three stimuli (mean \pm SE, n = 12 subjects) and results of Friedman test.

Behavioral parameters	Warble	Whistle	Entire song	Friedman test
Number of individual responding	10	12	11	
Latency (s) of first song	171.7 ± 61.9	78.7 ± 48	134.5 ± 52.3	NS
Number of songs	14.4 ± 5.7	8 ± 4.2	14.5 ± 3.6	NS
Latency (s) of first approach	186.7 ± 72.4	88.5 ± 47.2	145.3 ± 63.3	NS
Time spent (s) at >10 m	19.2 ± 11.3	33.1 ± 12.3	29.2 ± 18	NS
Time spent (s) at 5–10 m	67.9 ± 28.8	55.2 ± 13.4	82.3 ± 26.3	NS
Time spent (s) at <5 m	46.2 ± 21.3	82.9 ± 20.7	58.5 ± 33.1	NS

3.2. Repertoire analysis

As one measure of versatility, the entropy of the warble is significantly higher (Warble = -1.43 versus whistle = -2.5, Wilcoxon test Z = 4.6, p < 0.0005). Furthermore, the warble is more "complex" (based on the proportion of different syllables) than the whistle part (warble = 0.77 ± 0.05 versus whistle = 0.57 ± 0.04 , Wilcoxon test Z = 2.1 p < 0.05). Moreover, there is more sharing between whistle parts of different songs of the same individual than between warble parts (RSwarble = 1.15 ± 0.24 versus RSwhistle = 3.43 ± 0.49 , Permutation test: t = -4.34, p-value < 0.001). The birds belonging to the same group shared more syllables in the whistle part than in the warble part (RSwarble intra-pop = 0.022 ± 0.013 versus RSwhistle intra-pop = 0.21 ± 0.07 , Permutation test, N = 6, p = 0.001).

Warble and whistle parts seem to have completely different syllable repertoires as we never found syllable sharing between them.

3.3. Playback experiments

3.3.1. Territorial responses

The 12 tested males responded to at least one out of the three different broadcasted stimuli. Male blackcaps responded similarly to the 3 kinds of stimuli when all the behavioral parameters were analyzed independently (Table 2).

Two principal components were extracted explaining 64.1% of the variance of the responses. The latency before the first song and the time spent loaded more strongly on PC1. The number of songs and the latency before the first approach loaded more strongly on PC2 (Table 3). PC1 and PC2 scores were not significantly different in response to the different stimuli (Anova, PC1: F(2,12)=2.2, p-value=0.34; PC2: F(2,12)=0.17, p-value=0.92, Figs. 2 and 3). Although mean values are different, there are neither significant differences nor even a clear tendency as the individual variability is very important (see Figs. 2 and 3).

3.3.2. Song responses

Vocal responses overlapping the broadcasted songs are rare (6 out of 72 recorded songs in response to playbacks) and were not included in the analysis as it was impossible to perform acoustic measures on those signals. Only 6 out of 12 males sang in response to all the stimuli, and their vocal response was further analyzed.

Table 3Factor loadings of the response variables on the first (PC1) and second (PC2) principal components with eigenvalues and cumulative variances explained.

Behavioral parameters	PC1	PC2
Latency (s) to first song	-0.80	-0.17
Number of songs	0.22	-0.68
Latency (s) first approach	0.31	0.78
Time spent (s) at >10 m	0.63	-0.48
Time spent (s) at 5-10 m	-0.70	-0.38
Time spent (s) at <5 m	0.80	-0.24
Eigenvalue	2.32	1.53
Cumulative % variance explained	38.6	64.1

We selected the first four songs following the end of the playback. Males did not always sang the warble parts in response (28/72). We put 0 for the length of the part in this case. We found no statistical difference when comparing the acoustic characteristics of either the warble or the whistle parts for each of the songs sung in response to the 3 broadcasted stimuli (Table 4).

4. Discussion

4.1. Two parts with different acoustic parameters: different messages?

First, different messages could be encoded by different syllables as our analysis of the syllable content shows that the two parts do not share any syllable. In the gray-cheeked fulvetta, Alcippe morrisonia, whistled phrases are used for local recognition while harmonic phrases are used for species recognition (Shieh et al., 2013). In the pippits, Anthus spp., species identity is encoded in the terminal part of the song and individual identity in the introductory part (Elfström, 1990). Second, the warble is much more versatile and has a larger syllable repertoire size than the whistle. The repertoire size is often considered as a good predictor of mating success as it has been hypothesized that a larger repertoire size could be linked to higher male quality and that female could use this information to choose a better male. However, the correlation between repertoire size and mating success is not so clear and not universal (Forstmeier and Leisler, 2004; Soma and Garamszegi, 2011). Moreover, larger repertoires could also be used in intra-sexual context. In the great tit, Parus major, and the red-winged blackbird, Agelaius phoeniceus, intruders are less likely to enter territories when resident males have larger repertoires (Krebs et al., 1978; Yasukawa, 1981). Further experiments would thus be needed to study the role of the warble repertoire size in intra- and intersexual contexts. Third, a higher sharing of syllables between individuals of the same group is observed in the whistle compared to the warble. Sharing of syllables has been widely associated with group signatures and dialects (Dabelsteen and McGregor, 1996) and has been involved in the modulation of territorial defense behaviors (neighbor-stranger, Mundinger, 1982) as well as preferences in mate choice (Beecher et al., 2000; Espmark and Lampe, 1993). Syllables sharing would indeed facilitate the establishment of territories and therefore fasten access to a female (Payne and Payne, 1997). It has to be noted that in the blackcap song, the proportion of shared syllables is not as high as in other species. In the skylark, 83% of the syllable repertoire is shared between individuals (Briefer et al., 2009) while in the winter wren, Troglodytes troglodytes, 90% is shared (Camacho-Schlenker et al., 2011). A functional role of the shared syllables thus remains to be demonstrated in the blackcap.

4.2. Two parts with different acoustic parameters: different audiences?

The warble has a lower amplitude, a higher mean peak frequency, a broader bandwidth (especially with a much higher maximum frequency) compared to the whistle. The warble is likely

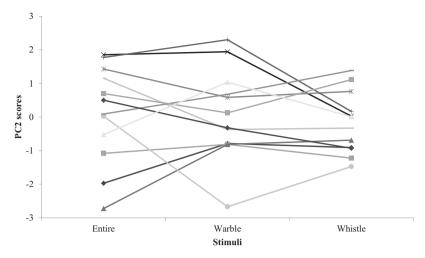


Fig. 3. Individual PC2 scores (N = 12) in response to the three boradcasted stimuli.

Table 4Comparison of acoustics parameters of the two parts of the songs in response to the three stimuli (Mean values ± SE) and results of Friedman test.

Response	Variables	Warble	Whistle	Entire	Friedman test
Warble	Mean frequency (Hz)	3907 ± 505	4078 ± 50	3827 ± 461	NS
	Bandwidth (Hz)	1713 ± 822	1709 ± 402	1748 ± 551	NS
	Min frequency (Hz)	3078 ± 308	3069 ± 255	3089 ± 365	NS
	Tempo	6.9 ± 1.8	6.3 ± 1.6	6 ± 1.5	NS
	Number of syllables	9.3 ± 4	9.2 ± 2	8.2 ± 3.5	NS
	Mean length (s)	0.56 ± 0.95	0.64 ± 0.77	$0.99\ \pm\ 0.81$	NS
Whistle	Mean frequency (Hz)	3166 ± 169	3181 ± 184	3200 ± 187	NS
	Bandwidth (Hz)	774 ± 116	842 ± 120	844 ± 124	NS
	Min frequency (Hz)	2781 ± 122	2748 ± 165	2767 ± 177	NS
	Tempo	6.3 ± 1.2	6 ± 1	6.2 ± 0.8	NS
	Number of syllables	13.7 ± 4	12.7 ± 4	13.4 ± 4	NS
	Mean length (s)	2.18 ± 0.88	2.13 ± 0.81	2.07 ± 0.69	NS

to be degraded over short distances in the forests where blackcaps live due to reverberation and attenuation whereas the whistle, with higher amplitude, lower frequency and less frequency modulation, has a larger capacity for long-range propagation as shown by propagation studies in this species (Mathevon et al., 2005). Such different capacities of propagation suggest that the warble and the whistle could be directed toward different audiences (Dabelsteen and McGregor, 1996).

It has been suggested that each part of the song could be directed to either a female or a male audience (Collins et al., 2009; Leedale et al., 2015) as in other species (Henry et al., 1994). The warble would be involved in female attraction (Collins, 2004) and the whistle in aggressive male-male interactions (Leedale et al., 2015; Sauer, 1955). These assumptions have been made because the warble is longer when females are fertile (Collins, 2004), and because the whistle becomes shorter and more stereotyped during male-male interactions (Sauer, 1955). Nonetheless, a recent publication showed that the whistle becomes in fact longer during male-male interactions (Leedale et al., 2015). The results of our playback experiments do support the idea that the whistle part of the song is involved in male-male competition since broadcasting the whistle alone is sufficient to trigger strong territorial behaviors. Males did not lengthen the whistle part in reply to the playbacks. However, the warble part is either absent or shortened in playback situations compared to spontaneous songs, suggesting that the whistle may encode important information related to male-male competition.

Interestingly, males also responded to the broadcast of the warble part alone. They approached the loudspeaker and some of them sung in reply with both warble and whistle parts, as in any other playback situation. Regardless of whether the warble part is primarily directed to females or not, the low-amplitude warble can thus be perceived and decoded by males, suggesting that the warble part can encode relevant information about the male emitter either in territorial competition or in the context of mate guarding.

Finally, it could also be proposed that both parts of the song, with different acoustic characteristics encoding potentially different messages and with a differential susceptibility to degradation. could be used in both intra- and inter-sexual contexts. According to the "acoustics adaptation hypothesis" (Rothstein and Fleischer, 1987), it could rather be postulated that, depending on the context, the two parts of the blackcap song could be directed to public versus private audiences, regardless of the sex of the audience as shown for low-amplitude and high-amplitude songs in other species (Reichard and Welklin, 2014). The "public information" could be the group and species identity and the "private information" could be the individual identity, the male quality, the motivational state and the breeding status. Further experiments are needed to validate such hypotheses, but segregating information in "private" and "public" parts of a single song appears especially wellsuited to an environment with dense vegetation like the blackcap's one.

Acknowledgements

This study was supported by the CNRS and the University of Paris Sud. J.L. is funded by a grant from the French Minister of Research and Technology. We thank Arthur Auriol and Sophie Dupont for their help in the field. We are very grateful to Gilles Faggio and Jean-Pierre Moussus for their help in catching and ringing birds

and to Thomas Corsi for English improvement. We thank the two anonymous referees for helpful comments on the manuscript.

References

- Beecher, M., Campbell, S., Nordby, J., 2000. Territory tenure in song sparrows is related to song sharing with neighbors, but not to repertoire size. Anim. Behav. 59, 29–37, http://dx.doi.org/10.1006/anbe.1999.1304.
- Briefer, E., Aubin, T., Rybak, F., 2009. Response to displaced neighbors in a territorial songbird with a large repertoire. Naturwissenschaften 96, 1067–1077, http://dx.doi.org/10.1007/s00114-009-0567-0.
- Brooks, R., Falls, J., 1975. Song features used in individual recognition. Can. J. Zool. 53, 1749–1761, http://dx.doi.org/10.1139/z75-101.
- Byers, B.E., 2011. Birdsong, migration and sexual selection: a skeptical view. Anim. Behav. 82, 2–4, http://dx.doi.org/10.1016/j.anbehav.2011.02.031.
- Camacho-Schlenker, S., Courvoisier, H., Aubin, T., 2011. Song sharing and singing strategies in the winter wren *Troglodytes troglodytes*. Behav. Process. 87, 260–267, http://dx.doi.org/10.1016/j.beproc.2011.05.003.
- Catchpole, C.K., Slater, P.J.B., 2008. Bird Song: Biological Themes and Variations, 2nd edition. Cambridge University Press.
- Collins, S.A., 2004. Vocal fighting and flirting: the functions of birdsong. In: Marler, P., Slabbekoorn, H. (Eds.), Nature's Music: The Science of Birdsong. Academic Press, pp. 39–79, http://dx.doi.org/10.1016/B978-012473070-0/50005-0.
- Collins, S.A., de Kort, S.R., Pérez-Tris, J., Tellería, J.L., 2009. Migration strategy and divergent sexual selection on bird song. Proc. R. Soc. B Biol. Sci. 276, 585–590, http://dx.doi.org/10.1098/rspb.2008.1011.
- Dabelsteen, T., McGregor, P.K., 1996. Communication networks. In: Kroodsma, D., Miller, E.H. (Eds.), Ecology and Evolution of Acoustic Communication in Birds. Cornell University Press, pp. 409–425.
- Elfström, T.S., 1990. Individual and species-specific song patterns of rock and meadow pipits: physical characteristics and experiments. Bioacoustics 2, 277–301.
- Espmark, Y., Lampe, H., 1993. Variations in the song of the pied flycatcher within and between breeding seasons. Bioacoustics 5, 33–65.
- Forstmeier, W., Leisler, B., 2004. Repertoire size, sexual selection, and offspring viability in the great reed warbler: changing patterns in space and time. Behav. Ecol. 15, 555–563, http://dx.doi.org/10.1093/beheco/arh051.
- Henry, L., Hausberger, M., Jenkins, P.F., 1994. The use of song repertoire changes with pairing status in male european starling. Bioacoustics 5, 261–266, http:// dx.doi.org/10.1080/09524622.1994.9753256.
- Hultsch, H., Todt, D., 1981. Repertoire sharing and song-post distance in nightingales (*Luscinia megarhynchos*). Behav. Ecol. Sociobiol. 8, 183–188.
- Krebs, J., Ashcroft, R., Webber, M., 1978. Song repertoires and territory defense in the great tit. Nature 271, 539–542, http://dx.doi.org/10.1038/271539a0.
- Leedale, A.E., Collins, S.A., de Kort, S.R., 2015. Blackcaps (*Sylvia atricapilla*) increase the whistle part of their song in response to simulated territorial intrusion. Ethology 121 (4), 403–409, http://dx.doi.org/10.1111/eth.12349.

- Marler, P.R., Slabbekoorn, H., 2004. Nature's Music: The Science of Birdsong.
- Mason, C.F., 1995. The Blackcap (Hamlyn Species Guide). Hamlyn, London.

 Mathevon, N., Aubin, T., Vielliard, J., da Silva, M.-L., Sebe, F., Boscolo, D., 2008.

 Singing in the rain forest: how a tropical bird song transfers information. PLoS

 One 3, e1580, http://dx.doi.org/10.1371/journal.pone.0001580.
- Mathevon, N., Dabelsteen, T., 2002. Why do songbirds sing intensively at dawn? A test of the acoustic transmission hypothesis. Acta Ethol. 4, 65–72, http://dx.doi.org/10.1007/s10211-001-0056-8.
- Mathevon, N., Dabelsteen, T., Blumenrath, S.H., 2005. Are high perches in the blackcap *Sylvia atricapilla* song or listening posts? A sound transmission study. J. Acoust. Soc. Am. 117, 442, http://dx.doi.org/10.1121/1.1828805.
- McGregor, P.K., 2005. Animal Communication Networks. Cambridge University
- Mundinger, P.C., 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: Kroodsma, D.E., Miller, E.H. (Eds.), Acoustic Communication in Birds. Academis press, New York, pp. 147–208.
- Nelson, D.A., 1989. Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*). J. Comp. Psychol. 103, 171–176, http://dx.doi.org/10.1037/0735-7036.103.2.171.
- Nelson, D.A., Poesel, A., 2007. Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song. Anim. Behav. 74, 1073–1084, http://dx.doi.org/10.1016/j.anbehav.2007.01.018.
- Payne, R.B., Payne, L.L., 1997. Field observations, experimental design, and the time and place of learning bird songs. In: Snowdon, C.T., Hausberger, M. (Eds.), Social Influences on Vocal Development. Cambridge University Press, pp. 57–84.
- Reichard, D.G., Welklin, J.F., 2014. On the existence and potential functions of low-amplitude vocalizations in North American birds. Auk 132, 156–166, http://dx.doi.org/10.1642/auk-14-151.1.
- Rothstein, S.I., Fleischer, R.C., 1987. Vocal dialects and their possible relation to honest status signalling in the brown-headed cowbird. Condor 89, 1–23.
- Sauer, F., 1955. Uber variationen der Artgesange bei Grasmucken. Ein beitrag zur Frage des Leierens des Monchsgrasmuckem. J. Ornithol. 96, 129–146.
- Shieh, B., Liang, S., Yuan, H., Chen, C., 2013. Experimental evidence that distinct song phrases in the grey-cheeked Fulvetta *Alcippe morrisonia* permit species and local dialect recognition. Ibis (Lond. 1859) 155, 32–41.
- Soma, M., Garamszegi, L.Z., 2011. Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. Behav. Ecol. 22, 363–371, http://dx.doi.org/10.1093/beheco/arq219.
- Tchernichovski, O., Nottebohm, F., Ho, C., Pesaran, B., Mitra, P., 2000. A procedure for an automated measurement of song similarity. Anim. Behav. 59, 1167–1176, http://dx.doi.org/10.1006/anbe.1999.1416.
- Wesołowski, T., 2011. Blackcap Sylvia atricapilla numbers, phenology and reproduction in a primeval forest—a 33-year study. J. Ornithol. 2, 319–329.
- Yasukawa, K., 1981. Song and territory defense in the red-winged blackbird (Agelaius phoeniceus). Auk 98, 185–187.