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Blackcaps (*Sylvia atricapilla*) increase the whistle part of their song in response to simulated territorial intrusion

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Abstract

Bird song is a sexually selected signal that serves two main functions, attracting a mate and deterring rivals. Different signal parameters may be important in advertising to females compared to advertising to rival males. Species solve the problem of this dual function in a variety of ways, one of which may be to have separate parts of song directed at male and female receivers. The blackcap song has two distinct parts, a complex warble, assumed to be directed at female receivers, followed by a louder and more stereotyped whistle putatively directed at males. We simulated territorial intrusions by broadcasting blackcap song in territories. Comparing songs sung prior, with those produced in response to playback, showed that the proportion of the whistle component of songs increased, but not the warble. This study thus provides empirical evidence that the whistle component of the blackcap song plays a prominent role in male–male competition. The warble component of the blackcap song may be directed at females, but this requires further testing.

Introduction

Intrasexual selection favours traits which increase success in same sex contests over access to mates, whereas intersexual selection favours those which increase attractiveness to mates (Andersson 1994). Most studies of sexual selection focus on these mechanisms in isolation (Hunt et al. 2009). However, the two types of sexual selection are unlikely to act independently, and how they interact is essential to understanding how sexual selection drives the evolution of secondary sexually selected traits. Although male–male competition and female choice can be reinforcing, there is increasing evidence to suggest that intrasexual and intersexual selection may not select for the same expression of a particular sexually selected trait (Moore & Moore 1999; Collins et al. 2009; Hunt et al. 2009).

Bird song is a signal involved in both inter- and intrasexual selection. While the dual function view of bird song is well supported (Catchpole & Slater 2008), direct, experimental evidence to demonstrate how bird song performs these potentially conflicting functions simultaneously is lacking. Many song birds appear to have different singing behaviours (Weary et al. 1994; Kunc et al. 2007), song types (Kroodsma 1981; Staicer 1989; Byers 1996; Kunc et al. 2006), specific notes (Vallet & Kreutzer 1995; Galeotti et al. 1997) or song parts (Lampe & Espmark 1987; Adret-Hausberger & Jenkins 1988) which are directed to receivers of each sex. Therefore, selection from male–male competition and female choice can act on song characteristics independently. However, in the breeding season, males will be signalling to both sexes simultaneously, leading to a trade-off between the conflicting demands on signal efficacy from male and female receivers. Although there is some evidence from playback studies that song varies adaptively according to whether the interaction is with a male or female (Weary et al. 1994; BeeBee 2004; Lohr et al. 2013; Geberzahn & Aubin 2014), most studies rely on observational and correlative data (Morse 1967; Lampe & Epsmark 1987; Staicer 1989; Wiley et al. 1994; Klit 1999).

The blackcap (*Sylvia atricapilla*) has a song of two distinct parts, a low-amplitude, complex warble with a wide frequency bandwidth, followed by a loud and relatively simple whistle (Hume 2002; Fig. 1). Both the warble and whistle contain a variable number and different types of notes, which may vary between songs (Collins et al. 2009). The warble is thought to play an important role in female attraction, and the whistle in territory defence (Collins et al. 2009). The blackcap's warble is longer at the start of the breeding season (Collins 2004) before pairs are established. The whistle becomes more stereotyped during aggressive male–male interactions (Sauer 1955) and occurs predominantly after egg laying (S. A. Collins, pers. observ.). Blackcaps employ a wide variety of migration strategies (Helbig et al. 2010), and the warble is longer in migratory compared to sedentary populations (Collins et al. 2009). Migratory populations are thought to be under stronger intrasexual selection pressure due to time constraints for breeding (Collins et al. 2009). However, the relationship between migration strategy and whistle duration is unclear, and its role in territorial disputes remains uncertain (Collins et al. 2009, 2011). As with studies on other species (Lampe & Espmark 1987; Klit 1999), the effect of intrasexual and intersexual selection on these song parts is based on assumptions generated from contextual associations (Collins 2004; Collins et al. 2009, 2011).

The dual role song plays in sexual selection in blackcaps has been disputed, and it was noted that direct, experimental evidence is lacking (Byers 2011). This study explicitly tests the function of the song structure in male–male competition in blackcaps, by comparing song composition before and after simulated territorial intrusion, using playback. We assume that during the pre-playback period, the birds sing spontaneously; while after playback, the male responds directly to a territorial intrusion. We predict that male blackcaps will change the composition of their song after playback, with a more pronounced effect on the whistle if this part of the song is involved in male–male competition.

Methods

The blackcap is a territorial oscine with a wide geographical range throughout Eurasia (Mason 1995). This study was conducted between 22 April and 9 June 2013, on blackcap populations in Manchester, UK, where we obtained nine successful trials and a population in Białowieża National Park, Poland where we obtained 15 successful trials. All trials were conducted between 5:00 h and 7:00 h or 17:00 h and 20:00 h (after the dawn chorus and outside the midday decline in activity) by the same experimenter.

Territory boundaries were assessed by monitoring each subject's movements prior to a trial. Individuals were observed until a minimum of three song posts was established, in order to roughly triangulate a minimum area which falls within an individual territory. Observations on each subject were divided into three periods: (1) 300 s baseline observation period, (2) 300 s control condition (60 s control stimulus followed by 240 s observation period) and (3) 300 s experimental condition (60 s blackcap stimulus followed by 240 s observation period). Thus, the start of the second playback is 240 s after the end of the first playback.

Trials using males in adjacent territories were separated by at least 2 d. During playback, a loudspeaker (FOXPRO® Fury) was placed within the territory and operated using a remote control (TX-500). Speaker volume was adjusted to 90–95 db, measured at 1 m from the source with a Sound Pressure Level Meter (Tenma, ST-805). Songs produced by the subject were recorded using a Marantz recorder (PMD 661) and a

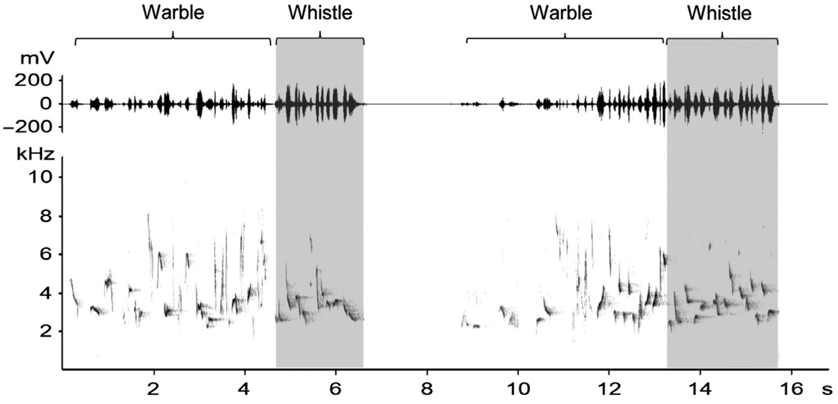

Fig. 1: Sonogram of a blackcap song before (left) and after (right) playback. The warble has a relatively low-amplitude and broad frequency range (unshaded). The whistle has a high amplitude and narrow frequency range (shaded). The proportion of whistle to warble increases in response to playback. Both songs were recorded from the same individual in Białowieża National Park, Poland.

directional microphone (Sennheiser ME67) at a sampling frequency rate of 44.1 kHz and a resolution of 16 bits per sample.

Only results from trials where a minimum of three songs was produced before and after playback were analysed. If this was not achieved on the first attempt, a second attempt with the same individual was made at least 2 d later.

As stimuli, we used 11 recordings taken from a larger database of blackcap songs from 48 individuals from three populations in Spain (Álava, Cádiz and Guadarrama, respectively). Songs from Iberian black caps are not known to differ in a meaningful way from those in Poland and England. Songs were selected on the basis of signal to noise ratio. Mean song duration was 3.83s (±0.09 SEM, n = 531) with a mean interval time of 2.21s (±0.08 SEM, n = 484). Stimulus song rate was based on this naturally occurring song rate, and each stimulus contained 10 songs, with at least three different songs sung by the same individual and a between-song interval of approximately 2–2.5 s. All stimuli were cleaned of background noise and standardised for amplitude in Avisoft-SASLab pro version 3.4 c (Avisoft Bioacoustics, Berlin, Germany).

Playback of Great tit *Parus major* song was used as a control, as previous playback experiments have been criticised for lack of control sounds (Kroodsma & Byers 1991). As great tits are not closely related to blackcaps and occur naturally in the habitat, this is a suitable control sound to ensure change in blackcap song composition is due to conspecific territorial intrusion rather than the experimental procedure. We predict no change in song composition between the pre-playback period and after the control playback.

The order in which the control and experimental songs were played was alternated to create 22 unique playback stimuli. Stimuli were uploaded directly onto the loudspeaker as uncompressed WAV files. Once all 22 stimuli had been used in a successful trial, they were reused for subsequent individuals. Although individuals were used from populations in the UK and Poland, the paired design controls for variation between individuals from different populations.

Songs were analysed in Adobe Audition (Adobe Systems, version 3, 2004). The following parameters were measured (Fig. 1): (i) total song duration (s), (ii) warble duration (s), (iii) whistle duration (s), (iv) from this, we calculated the proportion of whistle in the song, and average values were calculated for each male.

Collins et al. (2009) found that whistle complexity varied between migratory and residential populations in Iberia. Therefore, we also measured whistle complexity. We counted the number of different notes in the last three whistles before playback and the first three whistles after playback per individual in Avisoft-SASLab pro version 3.4 c (Avisoft Bioacoustics, Berlin, Germany). The relative complexity of each whistle was calculated as the number of different notes to total number of notes in the whistle (as in Collins et al. 2009). We then compared average relative whistle complexity in the baseline period and in the experimental condition per individual.

Differences in song duration, warble duration and whistle duration between the baseline period and the two conditions (control and experimental) were analysed using pairwise Wilcoxon's rank sum test with sequential Bonferroni correction (Rice 1989) for multiple testing. The same statistical tests were applied to analyse the proportional data (whistle duration/warble duration) determining the change in whistle duration in relation to warble duration irrespective of song length. To assess whether the order of the playback sequence affects warble and whistle duration in each condition, Welch two-sample *t*-tests were applied to compare the average response to a stimulus type played first to the average response to the same stimulus type played second. The same statistical tests were applied to analyse the differences in whistle complexity between the baseline period and the experimental condition. All statistical analyses were performed in R version 2.15.2 (R Core Team, 2014).

Results

We conducted 24 successful trials resulting in 1531 songs recorded from 24 individuals ($\bar{x}$ = 63.82 ± 4.94 songs per individual). Two males did not sing following the control playback, and the other 22 males did not show a difference in behaviour between baseline and control conditions (song duration: $V = 98$, p = 0.3705, n = 22, warble duration: $V = 88$, p = 0.2221, n = 22; whistle duration: $V = 143$, p = 0.6102, n = 22), so all subsequent analyses were conducted comparing only the baseline and experimental condition.

There was no difference in total song duration ($t = 1.30$, df = 21.28, p = 0.21), warble duration ($t = -0.12$, df = 19.73, p = 0.90) or whistle duration ($t = 0.22$, df = 20.10, p = 0.82) between males exposed to the control condition first and males exposed to the control condition second. Therefore, the order in which males are exposed to each condition did not affect these results.

There was no significant difference in song duration overall between the baseline period and the blackcap condition ($V = 182$, $p = 0.37$, $n = 24$, Fig 2a). There was a trend for a decrease in warble duration between the baseline period and the blackcap condition ($V = 213$, $p = 0.074$, $n = 24$, Fig. 2b). There was an increase in whistle duration in the blackcap condition compared with the baseline period ($V = 34$, $p < 0.001$, $n = 24$, Fig. 2c), and whistle duration increased in 20 of 24 individuals, with an average increase of 0.44 s (Fig. 2d). There was also a difference in the proportion of the whistle in the song between the blackcap condition compared with the baseline period ($V = 38$, $p < 0.001$, $n = 24$, Fig. 2e). There was no significant difference in relative whistle complexity between the baseline period and the blackcap condition ($t = -1.36$, df = 22, $p = 0.19$).

Discussion

Our results show that blackcaps increase the duration of the whistle and show a trend for a decrease in the warble in response to playback of blackcap song. Assuming that playback of blackcap song simulates an intruder, these results show that the whistle appears to function mainly in territory defence. These results provide experimental evidence that the whistle in the blackcap song is under selection from male–male competition and indicates that in blackcaps, different parts of the song perform different functions with respect to sexual selection.

Our results are not consistent with earlier suggestions that intrasexual selection selects for shorter, more stereotyped whistles and shorter songs in blackcaps (Sauer 1955) and other species (Adret-Hausberger & Jenkins 1988; Fessl & Hoi 1996), but these suggestions were not based on experimental evidence. However, it has long been known that during competitive encounters, a wide variety of singing strategies are employed across species (see Collins 2004; Catchpole & Slater 2008), with shorter and more stereotyped songs in some species (Catchpole 1983) and higher or lower switching rates (Vehrencamp 2000) or more complex repertoires (Mountjoy & Lemon 1991) in others. It appears that in the blackcap response to territorial intrusion simulated by playback results in longer, but not more stereotyped whistles. In the related spectacled warbler (*Sylvia conspicillata*), differences in song duration also did not result in a change in song complexity (Palmero et al. 2014). Nevertheless, our data contradict earlier findings by Collins et al. (2009) which suggest that male–male competition selects for more stereotyped whistles. However, the current study made within-individual comparisons in a specific behavioural context using controlled experiments, whereas Collins et al. (2009) compared song structure between populations.

The proportion of warble in the blackcap song decreased in response to playback, although this was not statistically significant. This change appears to be due to the increase in whistle duration. We did not test the role of the blackcap song in mate attraction, and thus, the role of the warble has yet to be explicitly demonstrated. One indirect way of testing female preference for song characteristics would be to compare the songs sung by extra-pair males with those of the males they cuckolded in the field (Poesel et al. 2006; Cramer et al. 2011). The difference in song structure between extra-pair males and social males may indicate the preference of females. Nevertheless, our study showed that the pre-playback songs consist predominantly of warbles, and overall, the suggestion that the warble may be more important in female choice, and less in male–male competition, is supported.

This study demonstrates that blackcaps adjust the emphasis of two song parts in response to an apparent change in the context in relation to intrasexual selection. Other species also change their singing strategies when confronted with an (simulated) intruder (Vehrencamp 2000). For example, nightingales (*Luscinia megarhynchos),* in contrast to blackcaps, reduce the relative use of whistles in their song when exposed to playback of conspecific songs (Kunc et al. 2006). Both sky larks (*Alauda arvensis)* and banded wrens (*Thryophilus pleurostictus*) reduce the intervals between syllables leading to denser song structures (Vehrencamp et al. 2013; Geberzahn & Aubin 2014). Thus, different bird species have adopted different strategies to address the intrasexual function of bird song.

Our findings are consistent with the idea that song in blackcaps serves a dual function, where one part serves to attract mates and the other serves to repel rivals. This balancing act between the two types of sexual selection on the same signal may be the mechanism by which genetic variation is maintained within a sexually selected trait (Moore & Moore 1999). This may explain why traits, which appear to be under strong directional selection, such as bird song, are still highly variable. The next step will be to test male response in terms of signal adjustment when singing to a female audience alone, and even more interesting to determine how males adjust their song when performing to a male and female audience simultaneously. How the trade-off situation is resolved may give an indication of the relative strength of inter- and intrasexual selection in a population.

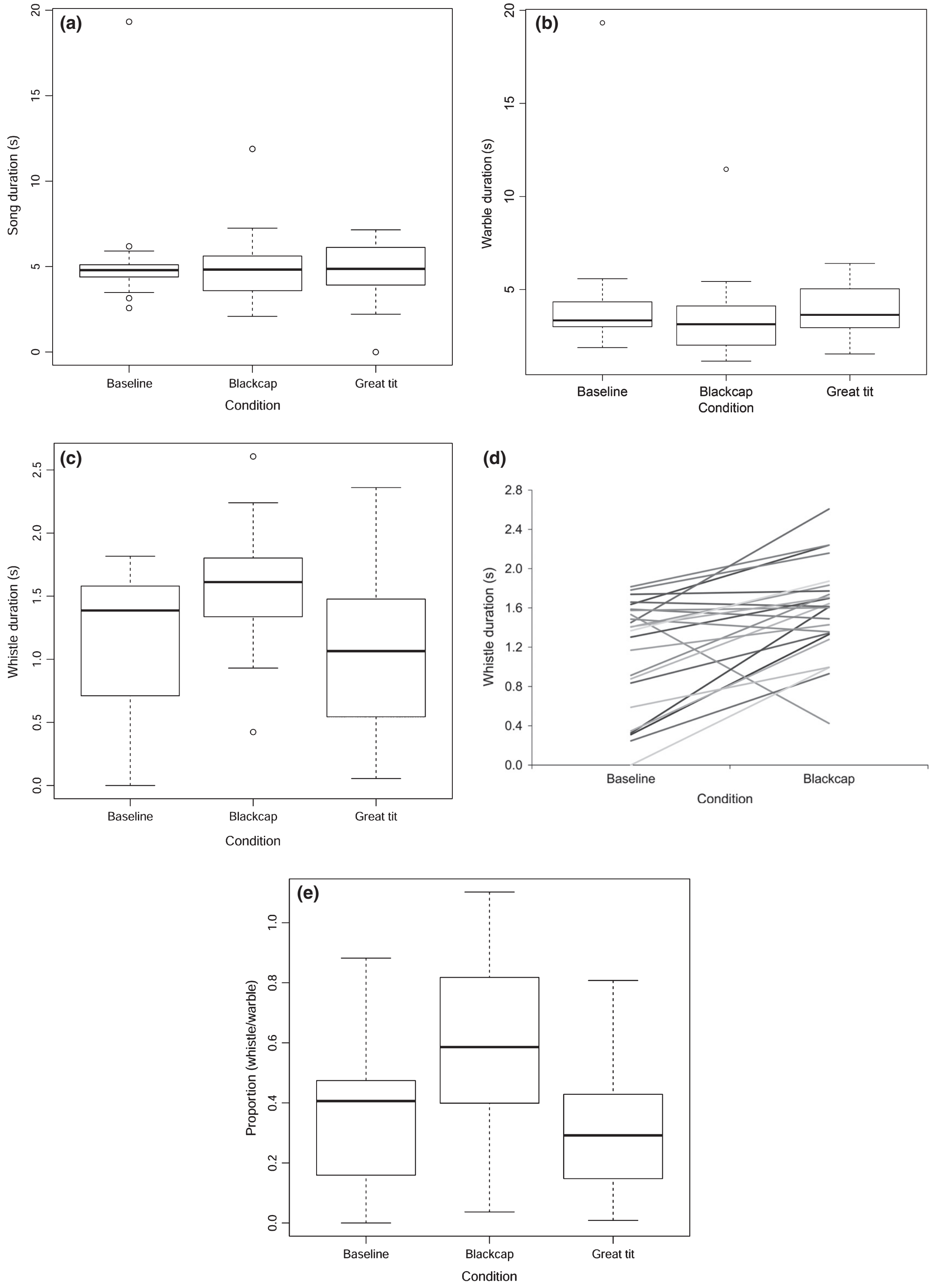

Fig. 2: The effect of playback on the song characteristics of male blackcaps. (a) Song duration (s); (b) Warble duration (s); (c) Whistle duration (s) in the baseline period (no playback), experimental condition (playback of blackcap song) and control condition (playback of great tit song); (d) Individual change in whistle duration (s) between the baseline period and the experimental condition; (e) Proportion of whistle to warble in the baseline period, experimental condition and control condition. Boxes represent IQR. Whiskers extend to ± 1.5 × IQR. Line across the box indicates the median. Outliers are represented by individual marks (n = 24).

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