Songs differing in consistency elicit differential aggressive response in territorial birds

Hector Fabio Rivera-Gutierrez*, Rianne Pinxten and Marcel Eens

University of Antwerp, Ethology Group, Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium
*Author for correspondence (hectorfabio.riveragutierrez@ua.ac.be).

Acoustic signals during intrasexual interactions may help receivers to establish the cost and benefits of engaging in a confrontation versus avoiding the cost of escalation. Although birdsong repertoires have been previously suggested as providing information during agonistic encounters, the cost (time/neural resources) of assessing large repertoires may decrease the efficiency of the signal for mutual assessment. Acoustic-structural features may, therefore, be used to enable a fast and accurate assessment during this kind of encounters. Recently, it has been suggested that the consistency of songs may play a key role during intrasexual interactions in bird species. Using a playback experiment in a colour-ringed great tit population, we tested the hypothesis that songs differing in consistency may elicit a differential response, indicating that the signal is salient for the receivers. Great tit males clearly responded more aggressively towards highly consistent songs. Our findings, together with previous evidence of increased song consistency with age in the great tit, suggest that song consistency provides information on experience or dominance in this species, and this phenomenon may be more widespread than currently acknowledged.

Keywords: birdsong; song consistency; sexual selection; intrasexual; interactions

1. INTRODUCTION

The evolution of sexually selected characters is driven by intersexual (mate) preference and/or intrasexual competition (increased ability to fight and deter rivals; [1,2]). These secondary sexual traits may signal a variety of aspects of individual quality, such as condition, dominance, age or fighting ability [3]. From an intrasexual perspective, potential rivals may use the expression of the signal to assess the costs and benefits of engaging in a confrontation versus avoiding the potential cost of escalation [4]. However, the elicited response may also depend on the perceived level of the threat or the aggressiveness of the opponent, given that an aggressive signal may also elicit an aggressive response [4,5].

Birdsong repertoire is an extensively studied sexually selected trait [2]. Although a large repertoire may provide an advantage during intrasexual interactions [3], its assessment by receivers requires time and neural resources that would proportionally increase with the size of the repertoires, thereby reducing the efficiency of the signal for mutual assessment during aggressive encounters [6]. This suggests that receivers may also use other aspects of song to gain a rapid and accurate assessment of the condition and/or fighting ability of their opponents. Indeed, different song-structural characteristics have been found to signal a variety of aspects related to individual quality or fighting ability in several bird species [7], offering cues for rapid assessment during intrasexual encounters. Among these structural traits, the stereotypic repetition of the songs (or song consistency) has recently drawn the attention of researchers. Recent studies revealed that consistent vocal performance correlates with reproductive success [8] and that song consistency increases with age and/or dominance in at least three different species [9–11]. These findings suggest that song consistency may be subject to sexual selection and could provide cues for potential rivals, eliciting different aggressive responses.

Using playback experiments is a classic approach for determining the role of birdsong during intrasexual interactions, during which the salience of a given signal is examined by the potential differential response of receivers towards the given stimuli [12]. Consistent differences in aggressive response towards playbacks have been previously reported for several bird species [12]. If song consistency provides information during intrasexual encounters, the use of playbacks with different versions of the same song that differ in consistency should elicit a differential aggressive response. At present, only one study has experimentally examined the differential response towards stimuli differing in consistency [10]. This study revealed that song consistency increases with age in banded wrens (Pheugopedius pleurostictus), and that individuals approached closer and sang at higher rates when exposed to the song of younger individuals (less consistent song). The authors argued that young birds may be perceived as equal competitors that may elicit a stronger response [10]. However, in a second experiment, the individuals responded partially when they were exposed to two different versions of the same song manipulated to differ in consistency. Although the males sang at higher rates when exposed to less consistent song, they did not differ in approach distance [10].

To test the hypothesis that song consistency will elicit a differential aggressive response in songbirds, we carried out a playback experiment in an established colour-ringed great tit (Parus major) population where a positive relationship between song consistency and age was reported previously [11]. We broadcasted two different versions of the same song, differing only in consistency within the natural range (as previously described for the species [11]), and scored the aggressive response of territorial males towards these two different songs.

2. MATERIAL AND METHODS

(a) Study area and general procedures

Data were collected in April 2009 in a colour-ringed great tit nest-box population located on the campus of the University of Antwerp,
Wilrijk, Belgium [11]. Nestlings and individuals caught for the first time received metallic-numbered rings, and all adults were ringed with a combination of three colour rings, enabling individual identification in the field.

(b) Playback experiment

The experiment was performed during the incubation period, when great tit males regularly visit their female to provide food and protection against intruder males and predators. At this time, the female is unlikely to affect the response of the male during playback. Playbacks were performed during the morning and under similar meteorological conditions (no rain, 10–12 °C). Using a paired design, a total of 28 breeding males were tested with two different versions of the same song differing only in consistency (high [HC] versus low consistency [LC]). A set of 13 different song types recorded in a non-neighbouring population were randomly assigned to the subjects (recording settings: PCM, 44 100 Hz, 16 bit, mono). The two versions of the songs were broadcasted in random order on two different days, v = 3-day period in between. An Anchor MiniVox loudspeaker was placed at an approximated distance of 5 m in front of the nestbox to increase the level of the threat and maximize the response [13]. The speaker was connected by a 20 m cable to an M-Audio MicroTrack 24/96 Professional Mobile Digital Recorder. Each playback session was recorded from an approximated distance of 20 m by using a directional microphone (Sennheiser Me67/K6) attached to a portable Marantz PMD660 digital recorder. After the speaker was placed, we first confirmed the presence of the male in the territory and then waited for 5 min to enable the birds to acclimatize to the experimental conditions before starting the experiment.

(c) Playback stimuli

The stimuli were created using Avisoft Pro software, v. 4.51 (Avisoft Bioacoustics, Berlin, Germany). From each of the 13 song types, we created two different versions (HC/LC) (figure 1). The highly consistent versions were created using only one complete strophe of approximately 3 s per song type. The LC versions were created using between 20 and 30 phrases per song type that were acoustically modified using the time/pitch conversion function in Avisoft Pro software. This feature changes the speed and pitch of the sound file by multiplying the timescale by a given factor without changing the sampling frequency. Values above 1 expand time (decrease pitch) and values below 1 reduce time (increase pitch). The phrases were randomly modified with a variety of factors ranging between 0.8 and 1.2 (figure 1b). Several phrases were appended in order to create strophes of approximately 3 s. Besides modification, the stimuli (HC/LC) were created in the same way. Phrases (LC) and strophes (HC) were based on their quality (signal-to-noise ratio), trimmed, filtered at 1500 Hz and their amplitude was normalized at 75 per cent of a volt. A silent gap of 3 s was added within strophes, which were repeated to create a 5 min loop song. Each stimulus consisted of a single song type. Pairs of stimuli (HC–LC) did not differ in the number of strophes, phrases or peak amplitude (paired t-test: all d.f. = 12, p > 0.1). Average spectrographic cross-correlation (SPCC), a measurement of song consistency used for great tits and other songbird species [11], was the only variable that differed between pairs of stimuli (paired t-test t = 12.2, d.f. = 12, 0.001; HC: 0.97 ± 0.005; LC: 0.67 ± 0.02), and it was within the natural range [11].

(d) Data analysis

Using previous studies as example [13,14], a total of five different behaviours were measured: latency, number of strophes sung, number of flights (short or long flights), closest approach distance and overlap coefficient (strophes overlapping/number of strophes sung [12]). These variables were reduced by means of a principal component analysis, from which three components were extracted, representing 75 per cent of the variance. The first component (hereafter called aggressiveness) was positively correlated with approach distance and negatively related to number of flights (loadings; approach distance = 0.868, number of flights = −0.844).

Values were transformed to the inverse (aggressiveness−1), indicating that higher values of the component represent more flights and shorter approach distance. The second component (singing behaviour (SB)) was positively correlated with approach distance and negatively related to number of strophes and overlapping (loadings: number strophes = 0.866, overlapping = 0.642). Finally, the third component (latency), was highly related to latency time (loadings: latency = 0.926). Using SPSS software for WIndows (v. 15 IBM, Chicago, IL, USA), we set a linear mixed model (LMM) with individuals as subject and treatment (HC–LC) as repeat. We tested for diagonal variance of repeats; treatment and order were set as fixed factors and age as covariate.

3. RESULTS

All tested birds responded by approaching, flying around and singing during the test. Age did not have a significant effect for any of the models and it was removed from the final models (all p > 0.6). Aggressiveness was the only variable that showed significant differences between treatments, being higher during presentation of highly consistent song (F1,28 = 17.23, p < 0.001, n = 28) and the interaction between order and treatment was also significant (F1,31.2 = 4.07, p = 0.05, n = 28; figure 2a). A linear model including only the first stimuli presented revealed that the aggressive response was significantly higher in individuals exposed to the highly consistent song (F1,25 = 6.2, p = 0.019, n = 14; figure 2b). SB and latency (L) did not differ between treatments, order or the interaction of these factors (SB: treatment: F1,48.95 = 0.43, p = 0.5; order: F1,48.95 = 0.77, p = 0.38, treatment * order: F1,48.95 = 0.82, p = 0.37; L: treatment: F1,32.68 = 1.48, p = 0.23; order: F1,32.68 = 0.9, p = 0.35, treatment * order: F1,32.68 = 1.62, p = 0.21; all n = 28).

4. DISCUSSION

Great tits differentially responded to two different versions of the same song that were manipulated to vary only in consistency. Overall, highly consistent songs elicited more aggression in resident males that approached closer to the speaker and also displayed more flights. Individuals had a less aggressive response during the second trial. Decreased behavioural response (habituation) during playback experiments has been previously reported for several bird species [15]. Although great tits seemed to habituate during
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Figure 2. Mean aggressive response towards highly consistent (HC) and low-consistent (LC) song during: (a) first and second trial, and (b) first trial.

our experiment, males responded differently to songs differing only in consistency during the first trial (figure 2b). LC songs during the first trial elicited less aggression than HC songs (figure 2b) and to a degree comparable to the responses (to both high and LC) during the second trial (figure 2a). Our results seem to contradict the previous experiment on song consistency, where less consistent song partly elicited a more aggressive response [10]. However, a recent review indicated that behavioural responses towards playbacks may differ between species and the differential response may help to confirm whether a song signal is salient across species [12]. Therefore, this study contributes to a growing body of literature on song consistency and age in this species [11], the present study strongly suggests that song consistency is perceived as a signal of experience and/or dominance.

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