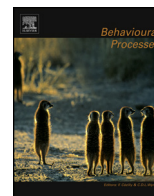




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Being angry, singing fast? Signalling of aggressive motivation by syllable rate in a songbird with slow song

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ABSTRACT

Syllable rate has been shown to play a role in male–male aggressive interactions and has been proposed to serve as a male quality indicator in several bird species. In those with fast syllable rates, males often increase rates when singing in aggressive context, and respond differently to test stimuli of varying rates. We asked whether the syllable rate fulfils a similar signalling function in the chiffchaff (*Phylloscopus collybita*), a songbird species with a slow syllable rate. We confronted 36 chiffchaff males with one of three playback types differing in syllable rate: control (non-manipulated rate), fast, or slow (artificially increased and decreased syllable rate, respectively). We recorded tested males' songs and behaviour before and during the experiment. Our results indicate that syllable rate might be an aggressive signal in chiffchaff. Males that physically attacked the loudspeaker during experiments sang faster songs spontaneously, and those that continued singing during the playback responded to fast and non-manipulated stimuli with substantial increase of syllable rate. Indirect evidence further suggests that syllable rate in chiffchaff is unlikely constrained by respiratory demands; thus, we propose that syllable rate in this species functions as a conventional signal of male aggressiveness rather than an index of quality.

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1. Introduction

Bird song has an important function both in mate attraction and territorial defence (Catchpole and Slater, 2008; Collins, 2004). It is well documented that both males and females are able to assess qualities of singers based on their song performance (Collins, 2004; Searcy and Nowicki, 2005; Ten Cate et al., 2002). This is only possible due to different costs (e.g., production costs, time costs, receiver retaliation) or constraints associated with the production of different song variants, which guarantees their signalling reliability (Gil and Gahr, 2002; Ten Cate et al., 2002; Vehrencamp, 2000).

Certain temporal characteristics of songs, especially of repeated elements (expressed as syllable or trill rate), are particularly suitable candidates to reliably reflect intrinsic male qualities (Vallet et al., 1998). Good performance of such song structures apparently depends on fine co-ordination of syringeal, respiratory, and vocal tract muscles, and has been documented to be constrained by

respiratory demands (Podos and Nowicki, 2004; Suthers et al., 1999). To allow continuous song renditions, birds insert mini-breaths between syllables (Calder, 1970; Hartley and Suthers, 1989). In species examined so far, longer syllables are accompanied by longer minibreaths (Cardoso et al., 2007b; Hartley and Suthers, 1989) or deeper (Wild et al., 1998), probably compensating for greater air loss during production of longer syllables (Franz and Goller, 2003; Hartley and Suthers, 1989). Physiological constraints on the rate of syllable delivery, experimentally documented by Podos (1996), predetermine the syllable rate as a candidate for an index signal of male quality.

The signalling function of the syllable rate has mainly been studied in combination with the song bandwidth, as a compound song performance trait (e.g. Ballentine et al., 2004; Cramer and Price, 2007; DuBois et al., 2011; Illes et al., 2006). Several studies found an increase in subjects' song vocal performances from a non-aggressive to aggressive context and speculated that this effect is due to singer emphasizing its own qualities (Beebe, 2004a,b; Cardoso et al., 2009; DuBois et al., 2009). Studies testing whether variation in the relevant parameters of song vocal performance is meaningful to receivers found different responses of females (Ballentine et al., 2004) as well as males (Cramer and Price, 2007; De Kort et al., 2009; DuBois et al., 2011; Illes et al., 2006), generally supporting the hypothesis that the vocal performance may signal male quality.

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Both parameters constituting performance (bandwidth and syllable rate) may be also treated independently, as slower trill types (i.e., longer syllables) may accumulate more frequency modulation intrinsically (Cardoso et al., 2007b). Therefore, syllable rate alone could be a parameter important for the signalling process in some species (Cardoso et al., 2007b). Within *Serinus* spp., characterized by very fast songs, syllable rate is apparently used for assessing singer's qualities by both females (Cardoso et al., 2007a; Drăgănoiu et al., 2002; Vallet and Kreutzer, 1995) and males (Cardoso et al., 2007a). To our knowledge, experiments testing if the changes in syllable rate are meaningful to rivals in bird species with much slower rates are lacking.

The chiffchaff (*Phylloscopus collybita*) is suitable for such a test, as it is a common species with a simple song of rather slow syllable rate (mostly ranging between 2.6 and 3.4 Hz; Linhart, unpublished data). Linhart et al. (2012) recently documented that this species that peak frequency of songs conveys information about the fighting ability, while song length probably signals motivation to escalate the conflict. However, males obviously modify also the song tempo during male–male interactions (Linhart and Jaška, pers. obs.). Therefore, we hypothesized that syllable rate might be another component of signalling in the context of male–male competition in chiffchaff. Given the relatively slow syllable rate of this species, it was nevertheless unclear whether the apparent increase is sufficiently demanding to signal male quality.

Based on these hypotheses, we made the following predictions to be experimentally evaluated. First, if syllable rate functions as a signal of aggression (Searcy and Beecher, 2009), it should increase during the playback stimulation, and it should correlate positively with the intensity of singer's response. Receiving males should also discriminate between stimulus types with different syllable rates. Second, if the syllable rate reflects male quality through song performance constrained by respiratory demands, longer syllables should be followed by longer syllable gaps. (However, other potential physiological constraints, such as those imposed by syrinx and oropharyngeal musculature or mechanics, would not be detectable by this approach.)

2. Materials and methods

2.1. Study site and population

Our study was conducted at the edge of České Budějovice, South Bohemia, Czech Republic (48°59.5' N, 14°26.5' E). The study area (ca. 1 km²) consists of a wooded marshland with ponds and stands of willow (*Salix*), birch (*Betula*), and aspen (*Populus*) trees, and some old oak (*Quercus*) avenues at the edges. The first chiffchaff males arrive to the area in the middle of March; after the peak of arrival by the end of March, there are about 80 breeding pairs. Males sing and defend their territories throughout the breeding season until the end of June. The first eggs are laid in the second half of April, hatching occurs from early May.

We conducted playback experiments on 36 males from April 22 to May 3, 2010. This period corresponds to fertile and post-fertile period of chiffchaff females, when the singing activity of males reaches its peak (Rodrigues, 1996). To avoid testing the same male twice, each bird was lured into a mist net (EcoTone, Gdynia) and colour-banded immediately after conducting playback experiments and subsequent song recordings. All birds were released in good condition immediately after banding and noting basic physical parameters (tarsus length and weight), within 5 min after capture. Banding and field playback experiments were approved by the Czech Bird Ringing Centre (licence no. 1067), and the Czech Animal Welfare Commission (permission no. 7956/2008–30).

2.2. Preparation of playback stimuli and experimental design

For preparation of playback stimuli, we used songs of 12 chiffchaff males recorded at our study site in 2006 or 2007, using a Marantz PMD660 solid state recorder (sampling frequency 44,100 Hz) and a Sennheiser ME67 directional microphone, equipped with a Rycote Softie windshield. For each male, we selected 1 min of high recording quality when the male was continuously singing (song rate: $\bar{x} \pm SD = 7.21 \pm 1.24$ songs min⁻¹). These songs were processed in Avisoft SASLab Pro software (Raimund Specht, Berlin) to prepare the playback stimuli. First, all recordings were down-sampled to a sampling rate of 22,050 Hz, band-pass filtered between 1500 Hz and 9000 Hz (well outside the frequency range of chiffchaff song: ca. 2500–8000 Hz) and standardized to 90% of maximum amplitude. This standardized set of songs was used to generate three experimental categories of manipulated songs: CONTROL (songs without manipulation), SLOW, and FAST, leading to $3 \times 12 = 36$ different playback stimuli. FAST stimuli were prepared by shortening of syllable gap by 0.04 s (i.e., 0.04 s long section between syllables was cut out of the recording). To create SLOW stimuli, we inserted additional section of silence between the syllables, thus increasing the syllable gap by 0.04 s. We chose the manipulation interval of 0.04 s because it roughly corresponds to half of the range between minimal and maximal mean values of syllable interval in spontaneous songs in the population studied (Fig. 1). Thus, we obtained experimental stimuli at and slightly beyond both extremes of natural variation in spontaneous syllable intervals (Fig. 1). Such songs were likely to be still recognized as conspecific, as chiffchaffs were shown to show species-specific responses even to songs with highly altered syllable interval (Schubert, 1971).

All playback experiments were conducted in the morning within 6 h after sunrise, i.e., between 6 and 12 AM. Each of the 36 experimental songs was played back only once, to a single chiffchaff male. Neighbouring males were never tested in two successive experiments. Song stimuli were played back in a loop for 5 min from a JBL Control 1x loudspeaker at a peak volume of 80 dB (A) SPL, measured at 1 m distance (using a Voltcraft SL-200 sound level meter, with Fast response setting). The loudspeaker was placed inside the tested male's territory. We started the playback from a shelter 10 to 15 m away from the loudspeaker while the focal male was in sight and singing.

The response behaviour of tested males was observed for 5 min during the playback. The following behavioural parameters were scored: time spent within 2 m from the speaker (s), latency of approach within 2 m (s), number of fly-overs (the focal male flying over the loudspeaker), latency of fly-overs (s), time spent attacking (focal male being in physical contact with loudspeaker), and latency of attack (s). Distance of the male from the speaker was estimated with the help of 2-m markers on the ground around the speaker. We particularly focused on occurrence of physical attacks, as these are the most intense and clearly aggressive type of response, while other responses that may be considered a general "agonistic" response do not have to be necessarily aggressive (Searcy and Beecher, 2009).

Some recent studies based on playback experiments used an artificial dummy or a taxidermic mount together with acoustic stimuli (Ballentine et al., 2008; Petrusková et al., 2007; Searcy et al., 2006; Turčoková et al., 2011), and even recommended using such visual stimulus to allow the tested bird to focus aggressive response (Akçay et al., 2011; Petrusková et al., 2008). We did not use mount in the experiments, however, our observations suggest that chiffchaff males respond similarly during experiments with and without a taxidermic mount. The loudspeaker attacks are very similar to mount attacks; the latter are nevertheless more severe (up to the intensity that may quickly result in a destruction of the

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