

Responses of a sub-oscine bird during playback: Effects of different song variants and breeding period

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Abstract

Vermilion flycatchers (*Pyrocephalus rubinus*) vary their song rate and song length across the breeding season. Males sing more and longer songs after nest construction than before. Here we explored the possibility that this variation is meaningful to territorial males. Using a playback approach, we tested several males with different variations in song output (i.e. variations in song length and song rate) in different periods of the breeding season (i.e. before and after the onset of nest construction). We found that males call more in response to playbacks of long and short songs before the onset of nest construction. However, after nest construction began they responded flying more when exposed to long songs than to short songs. These results show that vermilion flycatcher discriminates between different variants of song length, and suggest that males react to long songs as if they were more threatening signals than short songs, especially after the onset of nest construction. We did not find evidence of males discriminating between a high and a low song rate. We discuss some possible implications for song function in this sub-oscine species, and compare these findings with other results in oscine species.

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1. Introduction

In the well-studied oscine birds, there is interesting variation on whether species use different song types in different contexts (i.e. intra- and inter-sexual interactions), while others sing the same song type regardless of the context. For instance, great reed warbler's (*Acrocephalus arundinaceus*) long songs are mainly used in the context of female attraction, while short songs are used for territorial defence (Catchpole et al., 1986; Catchpole, 2000). Other species may use any of their structurally similar song types in both contexts, but song variation in structurally different parts may code different messages. For example, male and female chaffinches (*Fringilla coelebs*) differ in how they weigh the relative duration of the trill part of a song and the complex final phrase ('flourish'; Leitão and Riebel, 2003). On the other hand, how structural variation of song in sub-oscine birds functions in male–male competition and female choice has been little studied.

There are examples of sub-oscine species with a song repertoire, e.g. the great crested flycatcher, *Myiarchus crinitus* (Smith and Smith, 1996), or with a single song type like the alder flycatcher, *Empidonax alnorum* (Kroodsma, 1984) and our study species the vermilion flycatcher, *Pyrocephalus rubinus* (Smith, 1967; Ríos-Chelén et al., 2005; but see Ríos-Chelén and Macías-García, 2004). The great crested flycatcher may use different forms of songs when associating with a female or when interacting with a neighbouring male (Smith and Smith, 1996), and in some sub-oscines species females may sing in duet with her social partner as a mate defence strategy (Seddon and Tobias, 2005). However, it remains largely unknown how sub-oscine species, and especially those with a single song type, may use their only song type in different intra- and inter-sexual contexts. The evidence indicates that a single song type species like the alder flycatcher can discriminate between neighbours and strangers' songs (Lovell and Lein, 2004b), and also that they may use songs to recognize individual neighbours (Lovell and Lein, 2005). Therefore, it is possible that, among sub-oscines, even in a species with limited variation in song features among males (the alder flycatcher; Lovell and Lein, 2004a),

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a single song type can convey information to conspecifics males and have an intra-sexual function. In species like the alder flycatcher, or the vermilion flycatcher, that lack a repertoire, information regarding quality and motivation of the singer can only be coded in the form of variations within the single song type, for instance, by varying the number of elements in a song or varying the song rate (Wasserman and Cigliano, 1991).

The vermilion flycatcher's song has already been described (Smith, 1967; Ríos Chelén et al., 2005). During the breeding season, males sing mostly before and at dawn, and again at sunset, but singing at other times of the day (from perches or during flight displays) also occurs (De Benedictis, 1966; Smith, 1967; Archer, 1996; Ríos-Chelén and Macías-García, 2004). The vermilion flycatcher song is composed of several introductory elements (the first part of the song) followed by four elements (the second part). It has been found that males increase song length (adding introductory elements) and song rate after the onset of nest construction (Ríos Chelén et al., 2005). These authors also found a positive correlation between song rate and number of neighbours. The possible function of these changes is unknown, but the correlation described above, plus the fact that vermilion flycatchers seem to counter-sing with neighbours at dawn (Smith, 1967; Ríos Chelén, personal observation), suggests that song has a function in male–male communication.

Here we studied if vermilion flycatchers are able to discriminate between different song variants of their single song type. In other words, we tested whether males of this species respond differently to playbacks of long and short songs, and between a high and a low song rate, both attributes that have been shown to vary in nature (see above, Ríos Chelén et al., 2005). If this variation is meaningful to (male) receivers, we predict that territorial male vermilion flycatchers should respond differently to playbacks of long and short songs and between a high and a low song rate.

Work in oscine birds has shown that different aspects of song might be of different importance at different stages in the breeding season (Mace, 1987; Cuthill and Macdonald, 1990; Ballentine et al., 2003). We hypothesized that vermilion flycatcher males sing longer songs and at a higher rate after the onset of nest construction because this is a more efficient way to protect a resource (e.g. territory) in a period when it would be more costly to lose it (after nest construction: when an investment has been made to find, occupy and defend a territory), or because this is a period when the male's partner is potentially fertile and therefore paternity guarding may be in action. In either case, we expect longer songs and a higher song rate to be more threatening signals than short songs and a lower song rate. We therefore predicted that: (1) males should respond more to these more threatening signals (i.e. long songs and a higher song rate) irrespective of the period (i.e. before or after nest construction) and (2) if the second period (i.e. after nest construction) represents a more important time to protect a territory or to guard paternity, we expect that males should respond more strongly after nest construction than before nest construction.

2. Materials and methods

2.1. General

The experiments were carried out in 2003 in the Forest of San Diego Metepec ($19^{\circ}17.97'N$, $98^{\circ}14.60'W$), in the State of Tlaxcala, Mexico, where we have studied a colour ringed population since 2000. Part of this area is located within the campus of the Universidad Autónoma de Tlaxcala (UAT). The forest is composed mainly of *Pinus* sp. and *Eucalyptus* sp. with interspaced clearings and grasslands. Most birds in our study population appear to be migrants, leaving the territories around August or September, and returning in January.

2.2. Experimental songs

The songs used for the experiments were recorded in the same study site where the experiment took place 2 years earlier, in 2001. Songs were recorded at dawn with a Sennheiser ME66 microphone and a Marantz PMD221 cassette recorder, and digitized (number of bits = 16) using a 0 AliAudio Wave 5.10 sound card. Songs were high-pass filtered with a cut-off frequency below 2.8 kHz and sampled at a rate of 22,050 Hz using the Avisoft[®] SASLabPro software. We took care that during the experiment no individual was exposed to songs recorded from him or from a male known to have been his neighbour in any of the 4 years that we have studied this population (2000–2003). To prepare different treatments (see below) we used 64 different songs that came from 14 different males. All replicates were prepared with different songs and thus pseudoreplication was avoided (Kroodsma et al., 2001). Each individual was exposed to a paired treatment (long versus short songs and high versus low song rate). The high–low rate pairs (i.e. 25 and 15 songs/min) were made with the same song, a different one for each male, and thus any other variable other than rate was controlled for. Since the long–short song pairs were prepared with songs from different males we avoided the possibility that males could fail to discriminate as a result of listening to songs from the same individual (i.e. songs that shared the same individual identity attributes; Ríos Chelén et al., 2005). Treatments (Fig. 1) were prepared using the Avisoft[®] SASLabPro software. Long songs lasted in average 1.21 s (mean \pm S.E. = 1.21 ± 0.04) and short songs 0.61 s (mean \pm S.E. = 0.61 ± 0.02). Fig. 2 shows an example of long and short songs.

2.3. Playback

For the playback experiment we used a Mineroff SME-AFS loudspeaker connected with a 10-m cable to a Sony D-EJ621 CD player. The songs were played at a sound pressure level of 65–70 db measured at a distance of 8 m with a digital sound level meter (RadioShack, Cat. No. 33-2055). The experiment took place from 12 March to 2 July 2003, and from 08:00 to 13:30 h. To simulate a male intruding into the owner's territory, we located the loudspeaker in a tree judged to be well within the territory of the experimental male, and we took care to locate the

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