Does twitter song amplitude signal male arousal in redwings (*Turdus iliacus*)?

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Summary

Bird songs may vary in amplitude for several reasons. Variations due to differences in environmental conditions are well known but whether signal information varies with song amplitude is less well known. In some species quiet songs are heard as a soft twitter. These twitter songs are common in *Turdus* species and may be used during escalated close range encounters when a quiet song will attract less attention from others. Male redwings (*T. iliacus*) sing a terminating twitter part that is quieter and highly variable both between and within males compared with the introductory motif part. The twitter song of redwings, however, is often louder than the twitter in other *Turdus* species, especially during escalated song encounters. The seasonal variation in twitter duration also suggests that the twitter may signal increased aggression. We tested how male redwings responded to an assumed escalation in signalling. In an interactive playback experiment we increased the amplitude of the twitter songs we played back in response to an increase in twitter duration by the subject. Males gave stronger responses to louder twitter. This suggests that twitter amplitude may signal arousal in male redwings.

*Keywords*: song amplitude, twitter song, interactive playback, redwing, *Turdus iliacus*.

Introduction

Male songbirds defend territories by singing and these songs have evolved to become efficient in repelling competitors (Catchpole & Slater, 2008). When

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challenged, birds use multiple ways of communicating. They may change the temporal pattern and/or song content (reviewed by Todt & Naguib, 2000). This can be achieved by increasing the singing rate (Gottlander, 1987), and/or by increasing song length (Lampe, 1991; McGregor & Horn, 1992; Balsby & Dabelsteen, 2001). To address specific males during territorial disputes, males may overlap the songs of rivals or engage in matched counter-singing where they match song types to resemble the songs sung by a rival (e.g., Lemon, 1968; Dabelsteen et al., 1997). Overlapping and matched counter-singing have been found to correlate with aggressiveness and readiness to escalate interactions (e.g., McGregor et al., 1992; Dabelsteen et al., 1997; Vehrencamp, 2001). The same was also found for counter singing without matching the song type of the rival when answering (Hyman, 2003). Furthermore, in some cases males change the content of the song by switching to another vocalisation type (e.g., song sparrow Melospiza melodia, Beecher et al., 2000; Anderson et al., 2008). Some thrush species switch from full song (motif + twitter) to twitter song during vocal interactions, and this change to twitter song has been interpreted as an aggressive signal (Dabelsteen, 1985).

In the Turdus species these twitter songs are common and may be used during close range encounters (Dabelsteen et al., 1998). These songs are often quiet and can be very difficult to perceive by third parties (Dabelsteen et al., 1998). However, in the semi-colonial redwing (Turdus iliacus), the otherwise quiet twitter songs can become louder (as assessed by ear) during male–male interactions (Lampe, 1987). When breeding semi-colonially distances between singing males are often short and trying to hide an interaction from eavesdroppers by singing a quiet song, may be impossible. Redwings may, therefore, use amplitude, as a signal of quality or motivation.

Blackbird (T. merula) males responded with ‘strangled’ songs (i.e., twitter) and aggressive displays before flying off when played very loud full songs in the morning (Dabelsteen, 1981). Their responses to songs without a terminating twitter part were also less aggressive if the amplitude was lowered by 5 dB (Dabelsteen & Pedersen, 1992). In the laboratory blackbird males avoid singing from perches linked to matching or overlapping songs and an increased amplitude heightened the aversive effect in the one subject tested on amplitude differences (Todt, 1981). These studies suggest that song amplitude may have signal value during territorial encounters. Brumm & Todt (2004) suggested that vocal amplitude might be a signal in itself in