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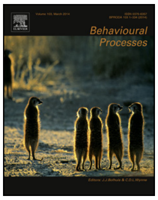

Timing vocal behaviour: Experimental evidence for song overlap avoidance in Eurasian wrens

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ABSTRACT

Timing during vocal interactions can play a significant role in terms of audibility as signal overlap may lead to masking of acoustic details for both of the interacting animals as well as for third-party eavesdroppers. Here we investigated timing aspects experimentally in Eurasian wrens (*Troglodytes troglodytes*) using non-interactive playback. We applied a randomized overlay method incorporating the temporal pattern of singing by the focal bird to establish a null model and to test observed patterns of overlap against this null model. We used different stimulus song rates but temporal response patterns always resulted in significantly lower levels of overlap than expected by chance. The male wrens avoided overlapping by timing their song starts predominately right after the end of stimulus songs, but they did not avoid being overlapped by the stimulus songs. The territorial males typically raised their song rates during and after playback with a tendency to shorten between-song intervals while keeping song durations unchanged. Higher song rates of the playback stimuli increased the extent to which responders were being overlapped by the stimulus songs. Our data provide experimental evidence for a timing ability in Eurasian wrens by which they reduce mutual interference during vocal interactions.

1. Introduction

Many animals use vocal interactions to mediate conflicts over access to resources (e.g., Bradbury and Vehrencamp, 1998; Espmark et al., 2000). A prominent and well-studied example concerns vocal interaction among territorial songbirds. Especially in temperate regions, male territorial birds may use singing interactions instead of physical conflicts to deter male competitors and to defend their territories for access to resources such as food and nesting sites, and by which they can also attract potential mates at the same time (Kroodsma and Byers, 1991; Collins, 2004). The timing of signals in such vocal interactions may serve specific communicative functions or carry information about the signaler's quality, status or motivation level (Todt and Naguib, 2000; Vehrencamp, 2000).

During vocal interactions, a vocal response to a competitor frequently results in some level of temporal overlap between the two series of songs, unless one or both of the two individuals exhibit active vocal avoidance. Song overlap occurs when a singer starts a song before its counterpart has terminated its song (Todt and Naguib, 2000), and may lead to communicative interference by auditory masking (Todt, 1981). Not being optimally informed due to signal masking may be detrimental for the vocal competitors, but also for third-party eavesdroppers (Todt and Naguib, 2000; McGregor and Peake, 2000). Overlap avoidance may therefore be a logical phenomenon that leads to alternated singing and is widely accepted as a singing strategy to avoid communicative interference in the context of intra-specific (e.g., Wasserman, 1977; Gochfeld, 1978; Popp, 1989) or inter-specific jamming (e.g., Cody and Brown, 1969; Ficken et al., 1974; Popp et al., 1985; Brumm, 2006; Planque and Slabbekoorn, 2008).

Patterns of song overlap between two competing birds can be affected through timing by one or both of the competitors. When competitor A starts a song during the song of competitor B, we consider A is overlapping and B is being overlapped. Overlapping and being overlapped may have different behavioural implications, for overlapping is often regarded as a potential signal of dominance or elevated aggression (e.g., Hultsch and Todt, 1982; Naguib, 1999; Otter et al., 1999; Mennill and Ratcliffe, 2004; Poesel and Dabelsteen, 2005; Kunc et al., 2007, Naguib and Mennill, 2010). An opposing view that considers overlapping as accidental and neutral has also been put forward recently (Searcy and Beecher, 2009, 2011). More data are needed for solving this controversy about the signal value of song overlapping, for which it is critical to use an appropriate null model to test for whether overlapping patterns are non-random (Naguib and Mennill, 2010; Searcy and Beecher, 2009, 2011). Faithful evaluation of whether overlapping

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occurs at levels that are above or below chance level is necessary for differentiating between adaptive, neutral or alternative hypotheses about the signal value of song overlap.

The Eurasian wren (*Troglodytes troglodytes*, formerly known as winter wren) is a good model species to study vocal interactions among competing males (e.g., Kroodsma, 1980; Kroodsma and Momose, 1991; Holland et al., 1998, 2000; Amrhein and Lerch, 2010). Male wrens are highly territorial, sing discrete and loud songs at a high rate with clear silent between-song intervals during their breeding season, and often occur at high densities. Eurasian wren singing is also readily triggered by playback of conspecific songs, while already active birds typically persist with high vocal activity in response to such a simulated territorial intruder (Holland et al., 2000; Erne and Amrhein, 2008). Recently, Camacho-Schlenker et al. (2011), in a study that focused on song repertoire use and song type sharing, suggested that neighbouring Eurasian wrens often overlap songs but also show a tendency to alternate songs by adjusting their timing. However, this study provided no statistical evidence for the alternating tendency in Eurasian wrens and a quantitative analysis with adequate replication and a test with an appropriate null model to assess overlap avoidance are currently still lacking.

In the current study, we tested experimentally whether Eurasian wren males avoid overlap with conspecific songs during the vocally simulated presence of a competitor to prove their timing ability during vocal interactions. We played back series of Eurasian wren songs with a manipulated and constant temporal pattern to territorial males without response-dependent adjustments (non-interactive playback). We assessed temporal overlap avoidance by analysis of the responders' tendency to start songs during a playback song (overlapping) and their tendency to stop after a playback song has started (being overlapped). We applied a novel method to predict chance levels of overlap as an null model for statistical testing in which we incorporated the temporal pattern of singing by the focal bird. By comparing predicted and observed overlap levels, we tested whether the subjects were actively avoiding song overlap or not.

2. Materials and methods

2.1. Subjects and study site

The Eurasian wren was formerly known as winter wren when it was still lumped with *Troglodytes hiemalis* of eastern North America and *Troglodytes pacificus* of western North America (Toews and Irwin, 2008). It is distributed from western Europe to eastern Asia and is one of the most common bird species breeding in the Netherlands, abundant in woodland, agricultural and urban areas (Jonkers, 2002). We recorded songs and tested behavioural responses to playback in wren territories away from heavy traffic. The song recordings and the playback experiments were conducted from March to May, 2010 and in March, 2011 in the city of Leiden and the adjacent villages of Oegstgeest and Warmond, the Netherlands (52°10′ N, 4°29′ E). Song recordings were collected during spontaneous singing activity between 5:00 and 10:00 am and we conducted playback experiments between 6:40 and 9:30 am. Individual territories were assessed by accumulated observations of movements (song posts switching) and vocal activities of male wrens. The territories were indicated on a map and visited repeatedly for song recordings before conducting the playback experiments. No birds used for playback experiment were direct neighbours. We could typically approach individual birds up to a distance of 6–16 m without disturbing them with our presence.

2.2. Stimulus recordings and manipulation

The song recordings were made with a Sennheiser ME67 directional microphone connected to a Marantz PMD661 digital recorder at a 44.1 kHz sample rate and 16 bit sample size. All recordings were processed with Avisoft SASLab Pro 5.0.14 (R. Specht, Berlin, Germany) and normalized to achieve comparable amplitude scales in spectrograms. We selected high-quality song recordings from different individuals in the study area, each for single use as stimuli in a non-neighbouring territory for the playback experiment to make all trials independent (c.f. Kunc et al., 2006, 2007). A single song was selected from each high-quality recording for generating playback stimuli as repetitive series with an artificially generated silent between-song interval (duration from the end of a song until the start of the subsequent song) using Avisoft SASLab Pro. We aimed at including a variety of song types and a variety of between-song interval lengths for different subjects. In total, 18 male wrens were tested with 18 different playback files from 18 different local individuals. The song types of the 18 playback files were different from each other. We controlled for the interval length which was held constant within each playback file. The choice of interval lengths were randomly selected (without using any one twice) from 18 values evenly distributed within the range of 3.46–10.90 s (mean = 7.01 s), which covered the range of natural between-song interval lengths of the local population well. Stimulus song durations ranged between 3.94 and 6.18 s (mean = 4.95 s). Song rates of the playback files ranged between 3.84 and 7.85 songs per minute (mean = 5.21 songs per minute).

2.3. Playback procedure

We chose male wrens for playback that were actively singing without vocally active neighbours. When a neighbour started to sing during the playback process, we discarded the experiment. We first collected a solo song bout recording for at least 3 min from each male. After the bird stopped singing for at least 1 min while we continued recording, we started broadcasting the playback file which was set to play for 5 min long. We continued recording for another 3 min after the end of playback. In this way, we collected a continuous recording without breaks including the periods before, during and after the playback in each experiment.

We used a Marantz PMD620 digital recorder connected to an Intertechnik M130 KX4 speaker with a Monacor IPA-10 amplifier for playback of song stimuli. The speaker was placed on the ground within the territory (in between the observed song posts) and close to the song post of the focal bird when it was singing (distances of 10–16 m to the focal bird). The broadcasting amplitude level was set at 90 dB sound pressure level at 1 m distance to the speaker, which is similar to a real wren singing volume (Brackenbury, 1979). We used a Radioshack sound level metre 33–2055 (A-weighted) to measure broadcasting amplitude. The same equipment used for the recording of song stimuli was used again for the recording of songs in response to playback. The directional microphone was pointed towards the bird and we tried to keep an angle perpendicular to the speaker for optimal separation of stimuli and response songs during recording. We were able to distinguish stimulus songs from response songs easily on spectrograms by song type characteristics and the stereotypic and repetitive nature of stimulus songs. In addition to the acoustic measures, we also estimated the minimum approach distance of the responding bird to the speaker and calculated the latency to sing after the playback started (the delay between the start of the first stimulus song and the start of the first responding song) during the playback as measures of response strength.