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Timing vocal behavior: Lack of temporal overlap avoidance to fluctuating noise levels in singing Eurasian wrens

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ABSTRACT

Many animals live in or near urban areas that have become increasingly widespread and noisy over the last century. Especially those species that rely heavily on acoustics for communication may be affected by these elevated anthropogenic noise levels. Many bird species that sing to defend their territories and to attract mates may have to exploit specific noise coping strategies to persist in such acoustically challenging conditions. Eurasian wrens (*Troglodytes troglodytes*), like several other bird species, have been shown in a previous experiment to time their vocalizations such that they avoid overlap with other singing birds. Here, we tested whether Eurasian wrens also time their songs to avoid overlap with fluctuating anthropogenic noise. However, we did not find any evidence in favor of this potential phenomenon. Territorial wrens persisted in singing without temporal adjustments in noisy territories with 'natural' fluctuations of traffic noise levels as well as during experimental exposure to intermittent white noise.

1. Introduction

The ongoing urbanization of our planet typically includes a turn-over of natural habitat, but also an increase in human activities and associated noise levels. Such anthropogenically raised noise levels may yield detrimental effects to animals within and beyond the human-altered urban habitat through deterrence, disturbance, and physiological stress, but also by interference of acoustic signals (e.g., Slabbekoorn and Ripmeester, 2008; Barber et al., 2010; Slabbekoorn et al., 2010). For example, bird song is of great importance in mate attraction and territorial defense, and signal interference may result in negative fitness consequences for breeding individuals (e.g., Habib et al., 2007; Francis et al., 2009; Halfwerk et al., 2011a; Schroeder et al., 2012). As environmental noise levels rise artificially, both signal producers and receivers may suffer from detrimental threshold shifts for detection and recognition (e.g., Lohr et al., 2003; Brumm and Slabbekoorn, 2005; Pohl et al., 2009, 2012).

However, studies have shown that animals have access to a variety of behavioral strategies to counteract noisy conditions and avoid or reduce signal interference. One of those strategies concerns the Lombard effect: singing or calling louder with increasing noise levels. This mechanism based on immediate auditory feedback is found in animals as well as humans and has a positive effect on signal-to-noise ratios at the receiver (Lombard, 1911; Brumm and Todt, 2002; Brumm and Zollinger, 2011; Eliades and Wang, 2012). A second strategy to counteract noisy conditions is spectral avoidance of masking noise. For example, many bird species have been shown to sing relatively high-frequency songs at places with much low-frequency noise (e.g., Slabbekoorn and Peet, 2003; Fernández-Juricic et al., 2005; Slabbekoorn and den Boer-Visser, 2006; Brumm and Slater, 2006; Parris and Schneider, 2009; Nemeth and Brumm, 2009; Francis et al., 2011; Potvin et al., 2011). For several species there is now also experimental evidence for the capacity to rapidly adjust pitch to currently fluctuating noise conditions (e.g., Halfwerk and Slabbekoorn, 2009; Verzijden et al., 2010; Gross et al., 2010; Bermúdez-Cuamatzin et al., 2011; Montague et al., 2013; McLaughlin and Kunc, 2013).

A third signaling strategy that could alleviate the pressure from masking noise concerns temporal adjustment. For example, common marmosets (*Callithrix jacchus*) produce longer calls under more noisy conditions, which improve signal detection probability through temporal summation (Brumm et al., 2004). Two other examples of such temporal adjustments in naturally noisy places are found in chaffinches (*Fringilla coelebs*) close to noisy rivers (Brumm and Slater, 2006) and king penguins (*Aptenodytes patagonicus*) in noisy colonies (Lengagne et al., 1999). Both bird species raise the chances to get their vocal message across by using higher vocal repetition rates during periods with naturally elevated noise

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levels. A case of temporal adjustment to anthropogenic noise has been found in European robins (*Erithacus rubecula*), which were reported to have more nocturnal singing activity related to day-time traffic noise levels (Füller et al., 2007). House sparrows (*Passer domesticus*) and spotless starlings (*Sturnus unicolor*) were also shown to respond to anthropogenic noise by starting to sing earlier on days of experimental exposure (Arroyo-Solís et al., 2013).

Most of these earlier studies focused on natural and gradually fluctuating ambient noise or on relatively long-term effects of anthropogenic noise. However, anthropogenic noise is often intermittent with short-term fluctuations, such as noise caused by car traffic within cities, over-flying airplanes, or all sorts of industrial machinery. Bermúdez-Cuamatzin et al. (2009) reported an upward shift in minimum frequency of the same syllable type in house finch (*Carpodacus mexicanus*) males during such momentary increases of traffic noise, but did not reveal whether strategies other than pitch modulation were used by the house finches to escape from the short noise bursts. Examples from natural situations reveal that at least some animal species are capable of avoiding intermittent sound events by short-term temporal adjustment of vocal activity. For example, field crickets (*Acanthogryllus fortipes*) and African reed frogs (*Hyperolius marmoratus*) actively avoid call overlap with neighboring males in their natural habitat. Experimental evidence revealed that individual male crickets and frogs adjust calling rate by which they exploit the silent intervals in between playback of calls (Cade and Otte, 1982; Grafe, 1995).

Several songbird species are also reported to avoid song overlap with conspecific competitors (e.g., Wasserman, 1977; Gochfeld, 1978; Yang et al., 2014) and even with different species (e.g., Ficken et al., 1974; Popp et al., 1985; Brumm, 2006). The avoidance of song overlap presumably prevents jamming or acoustic interference and is apparently a widespread phenomenon within and among bird species (Planqué and Slabbekoorn, 2008; Searcy and Beecher, 2009; Naguib and Mennill, 2010). Such timing ability could also be very useful in the context of anthropogenic noise. However, the examples so far to demonstrate short-term vocal timing to escape artificial and intermittent noise conditions concern only indoor experiments with primates, cotton-top tamarins (*Saguinus oedipus*) (Egnor et al., 2007) and common marmoset (*Callithrix jacchus*) (Roy et al., 2011), which were able to insert their calls into silent intervals in artificial bursts of white noise.

It may be expected that more animal species will be capable of timing their vocal activity around anthropogenic noise fluctuations given the taxonomically widespread ability to avoid certain sound fluctuations. It may be especially likely that some bird species will be capable of avoiding short-term fluctuations in traffic noise as there are many examples of birds timing their songs to vocalizations of other singing birds. In a previous study, we revealed experimentally that male Eurasian wrens (*Troglodytes troglodytes*) have the ability of temporal avoidance during vocal interactions (Yang et al., 2014). The wrens achieved significantly lower overlap than expected by chance with a playback series of conspecific songs. It remains untested whether such a dynamic timing capacity can also be used for avoiding interference with short-term fluctuations in anthropogenic noise.

In this study, we first examined Eurasian wren singing in urban territories with 'naturally' fluctuating traffic noise conditions. We expected the wrens to show temporal avoidance of noise peaks from passing cars by adjusting song duration and/or between-song interval length. Singing birds could stop a song earlier or wait for longer to start the next song when noise levels are relatively high. Secondly, we exposed singing Eurasian wrens in relatively quiet territories with artificially generated intermittent white noise to test whether they avoid temporal overlap with anthropogenic noise in the same way as they do with playback of conspecific songs. As spectral avoidance could reduce the need for temporal avoidance (Planqué and Slabbekoorn, 2008), we used white noise instead of traffic noise.

2. Methods

2.1. Study area and Eurasian wren song

This study was conducted in residential areas and urban parks in the city of Leiden and the connected villages of Oegstgeest and Warmond in the Netherlands (52°10′ N, 4°29′ E). Eurasian wrens are one of the most common bird species breeding in the Netherlands (Jonkers, 2002) and they are also abundant within and around our study area. We recorded singing males in territories with fluctuating noise conditions near busy roads and we recorded singing males before, during and after experimental exposure in relatively quiet territories away from busy roads. 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 were visited repeatedly for song recordings before the days of experimental exposure. We only used males from non-neighboring territories for experimental testing.

Songs of Eurasian wrens typically consist of a series of rapidly modulated elements with several repetitive trills connected by unrepeated components (e.g., Kroodsma, 1980; Holland et al., 2000; Amrhein and Erne, 2006; Camacho-Schlenker et al., 2011; Yang et al., 2014). In our study population, the spectral bandwidth of Eurasian wren songs ranged from 2.5 to 9.2 kHz (measurements for natural song recordings from 22 territories, which were collected between 5:00 and 10:00 am from March to May 2010). The average song duration for regular singing bouts in our study population was: 4.22 s (±0.69 SD, $n = 22$), the average between-song interval length was: 7.18 s (±1.55 SD, $n = 22$) and the average duty cycle (duration from the start of a song until the start of the subsequent song) was: 11.39 s (±1.79 SD, $n = 22$).

2.2. Analyses on songs in noisy territories

For the observational study, we recorded 12 Eurasian wrens in territories close to busy roads in which passing motor vehicles generated average noise levels between 50 and 66 dB(A) within the territories (maximum noise levels ranged between 58 and 74 dB(A), $n = 12$). We also recorded 12 individuals in quiet territories away from busy roads in which the average ambient noise levels were all lower than 50 dB(A). Song recordings in both noisy territories and quiet territories were made between 7:00 and 9:40 am from May 23rd to June 28th, 2010. We used a Radioshack 33-2055 sound level meter (Slow response time, A-weighted) to measure the ambient noise level when the focal bird was not singing. We took a 1-s sample measurement every 10 s in a continuous 5-min period after each song recording to assess the range of noise fluctuation within each territory.

To investigate whether "naturally" fluctuating traffic noise levels affected song timing in Eurasian wrens, we compared the song rate, song duration and between-song interval length in noisy territories with those in quiet territories. We also compared the song timing parameters at the most noisy and most quiet moment within each recording from the noisy territories. We measured the relative amount of sound energy present in the ambient noise in root mean square (RMS-value) within a 3.5-s period (which is about half of the average between-song interval length) in our recordings both before and after each song to assess the instantaneous noise levels at the moment of the song. For comparisons in song duration, we used the averaged noise levels of both pre- and post-song 3.5-s periods. For between-song interval length comparisons, we used the averaged noise levels of post-song and the next pre-song 3.5-s