



Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries



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ARTICLE INFO

Article history:

Received 1 May 2013

Initial acceptance 29 May 2013

Final acceptance 11 September 2013

Available online 14 November 2013

MS. number: 13-00371

Keywords:

anthropogenic noise

birdsong

domestic canary

masking

mate choice

Serinus canaria

Increasing levels of anthropogenic noise represent a challenge for animals living in urban areas and birds, especially, may suffer from noisy conditions as they use singing to attract mates. Most anthropogenic noise is low in frequency and singing at high frequencies under noisy urban conditions may avoid masking and thus be a good strategy for breeding success in cities. Despite comparative, correlational and some experimental studies supporting this hypothesis, empirical studies on the impact of noise on sexual behaviour are largely lacking. Domestic canaries, *Serinus canaria*, provide an excellent model system to test unequivocal sexual responsiveness as receptive females perform copulation solicitation displays (CSD) to male song. We have previously shown that CSD rate was higher for low- than for high-frequency songs. In the current study, we tested whether a typical urban noise spectrum, with a bias towards low frequencies, could undermine sexual preferences. Using overlapping and alternating noise exposure regimes while broadcasting male songs we found that masking by urban noise reduced female responsiveness to low-frequency attractive songs. Under the same conditions the responsiveness to high-frequency songs remained unaffected and, consequently, the sexual preference for low- over high-frequency songs had faded because of the urban noise. We discuss to what extent our results can be extrapolated to other wild bird species and speculate about the adaptive value of the typical upward shift in frequency found in many city birds.

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Birds use songs for both defending territories and attracting mates (Bradbury & Vehrencamp, 2011; Catchpole & Slater, 2008) and birdsong is known to be a sexually selected trait (Andersson, 1994; Ryan & Keddy-Hector, 1992). Birds can use the acoustic characteristics of songs to recognize conspecifics (Mathevon et al., 2008) and assess an individual's relative threat as a potential competitor (Linhart, Slabbekoorn, & Fuchs, 2012) or suitability as a social or sexual partner (Draganoiu, Nagle, & Kreutzer, 2002). These vocal communication processes may be hampered by both abiotic (Brumm & Slater, 2006) and biotic noise (Aubin & Jouventin, 1998) and especially by anthropogenic noise in an increasingly urbanized world (Barber, Crooks, & Fristrup, 2009).

One important factor associated with the urban environment is the typically low-frequency noise generated by traffic, construction, industrial or recreational activities. Several recent review papers

have stressed the challenge that animals face in noisy urban environments, addressing, on the one hand, the negative impacts of noise exposure on vocal communication (Barber et al., 2009; Dooling & Popper, 2007; Kight & Swaddle, 2011; Warren, Katti, Ermann, & Brazel, 2006) and, on the other, strategies by which animals may counteract detrimental effects of masking (Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006; Slabbekoorn, 2013).

Empirical studies have revealed that noise interferes with vocal behaviours that are critical to the success of individual reproduction and population survival. Ambient noise has, for example, been shown to affect the detectability of acoustic signals in a variety of vertebrate taxa, including frogs, fish and birds (Pohl, Slabbekoorn, Klump, & Langemann, 2009; Vasconcelos, Amorim, & Ladich, 2007; Wollerman, 1999). In each of these taxa, there are also reports on how noise interference can result in important changes in agonistic interactions between competing males (Bee & Swanson, 2007; Sebastianutto, Picciulin, Costantini, & Ferrero, 2011) or between vocalizing males and responding females (Appeltants, Del Negro, & Balthazart, 2002; Halfwerk, Bot, & Slabbekoorn, 2012). A choice test that can reveal either a social or a sexual preference has shown that white noise can undermine a female's preference for

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her own mate in zebra finches, *Taeniopygia guttata* (Swaddle, McBride, & Malhotra, 2006; Swaddle & Page, 2007). These kinds of studies reveal aspects of the behavioural mechanism by which noisy conditions can lead to a reduction in male pairing success (Gross, Pasinelli, & Kunc, 2010; Habib, Bayne, & Boutin, 2007) and in reproductive output (Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011; Schroeder, Nakagawa, Cleasby, & Burke, 2012). However, there are also behavioural strategies that allow some species to avoid or at least reduce the detrimental effects of noisy conditions.

Birds are especially well known to exhibit noise-dependent behavioural changes that may help them to communicate more efficiently and still reproduce under noisy urban conditions. The masking impact of the ambient noise is determined by the signal-to-noise ratio on the receiver's side and there are several strategies that may improve this ratio. Singing birds may, for example, increase signal redundancy, by which relatively silent gaps may become exploited (Brumm & Slater, 2006), increase signal amplitude in response to an increase in noise level (the Lombard effect, Brumm & Zollinger, 2011), decrease the distance to the receiver when it is noisy (Halfwerk et al., 2012), exploit the quieter periods of the day or night (Fuller, Warren, & Gaston, 2007) and avoid the frequency range predominantly covered by the noise (Slabbekoorn & Peet, 2003). Multiple vocal parameters may be interrelated and change at the same time (Montague, Danek-Gontard, & Kunc, 2013; Nemeth et al., 2013).

Singing at higher frequencies under noisy than under quiet conditions has been found in many urban bird species. Noise level-dependent song frequency use is a consistent finding of correlational (Luther & Derryberry, 2012; Potvin, Parris, & Mulder, 2011; Slabbekoorn & den Boer-Visser, 2006) and experimental exposure studies (Bermudez-Cuamatzin, Rios-Chelen, Gil, & Garcia, 2011; Gross et al., 2010; Halfwerk & Slabbekoorn, 2009; Montague et al., 2013; Verzijden, Ripmeester, Ohms, Snelderwaard, & Slabbekoorn, 2010). The underlying mechanism of the noise-dependent increase in, usually, the minimum frequency or the peak frequency of the lowest song notes varies between species (Slabbekoorn, 2013). It has, for example, been shown to occur by noise-dependent shifts of the same low syllable (Bermudez-Cuamatzin et al., 2011; Bermudez-Cuamatzin, Rios-Chelen, Gil, & Garcia, 2009) but also by a noise-dependent tendency to switch from relatively low-frequency to higher-frequency song types from the available repertoire (Halfwerk & Slabbekoorn, 2009).

Singing at higher frequencies under noisy than under quiet conditions may reduce masking by typically low-frequency traffic or industrial noise. Comparative and correlational studies based on occupancy patterns of breeding birds indeed suggest critical benefits for high- over low-frequency singers in noisy habitats (Francis, Ortega, & Cruz, 2009; Goodwin & Shriver, 2011; Hu & Cardoso, 2009). Psychoacoustic studies in the laboratory on great tits, *Parus major*, also reveal better discrimination abilities for high- than for low-frequency songs under urban noise conditions (Pohl et al., 2009; Pohl, Leadbeater, Slabbekoorn, Klump, & Langemann, 2012). Singing at low frequencies appears to be an important sexual signal in this species as paired males of a nestbox population were reported to sing at their lowest frequencies at the peak of female fertility and low-frequency songs were associated with high female fidelity (Halfwerk, Bot, et al., 2011). An experimental exposure test revealed a negative impact of typical urban noise on the low- but not the high-frequency song types (Halfwerk, Bot, et al., 2011). These results suggest the noise is interfering with a sexual signal under natural conditions, although the behavioural measurement in this study (female leaving the nestbox in response to male song) is not an unequivocal measure of sexual preference.

A well-established model system to test whether urban noise can affect sexual preferences for low- over high-frequency songs is

available in domestic canaries, *Serinus canaria* (Leboucher et al., 2012; Leboucher, Kreutzer, & Dittami, 1994). Receptive female canaries adopt an unequivocal sexual behaviour in response to song playback: a stereotypic copulation solicitation display (CSD). Quantification of the CSD response to sequential exposure of male song has revealed that females consistently prefer special, so-called A-phrases that are characterized by both a large syllable bandwidth and a high syllable repetition rate (Draganoiu et al., 2002; Vallet, Beme, & Kreutzer, 1998; Vallet & Kreutzer, 1995). Furthermore, it has also been shown, with artificially modified songs, that female canaries prefer A-phrases with relatively low frequency ranges over those with high frequency ranges (Pasteau, Nagle, & Kreutzer, 2007) and that their sexual responsiveness decreases with increasing levels of white noise (Appeltants et al., 2002). The impact of typical urban noise spectra on sexual preferences has not yet been investigated in canaries. We are also not aware of any direct test for the impact of noise on the sexual responsiveness for spectral song variation in any bird species.

In the current study, we investigated the effect of masking under noisy conditions on sexual responsiveness in two experiments with captive canaries. In experiment 1, we assessed the level of urban noise required to reduce female sexual responsiveness to low-frequency A-phrases (1–5 kHz). We then (experiment 2) used the noise level found to decrease female responsiveness most clearly in experiment 1 to test the impact of masking on female sexual preferences for low-frequency (1–5 kHz) A-phrases over high-frequency (3–7 kHz) A-phrases. Owing to the spectral characteristics of urban noise, low-frequency songs should be more masked than high-frequency ones and we expected that the preference would disappear or even reverse in the noisy condition. Such a result would show that urban noise can undermine sexual selection for low-frequency songs.

METHODS

Subjects and Housing

We used 41 breeding domestic canary females, which were all reared in our own breeding facilities at the University of Paris Ouest Nanterre and were not previously exposed to urban noise stimuli. Our laboratory stock is an outbred group of birds of heterogeneous genetic background. For both experiments, females were kept in individual cages (35 × 20 cm and 23–25.5 cm high) equipped with two perches and placed in individual sound-proof chambers (68 × 51 cm and 51 cm high). We provided females ad libitum access to water, food (seeds, mash and apple) and calcium (cuttlebones) and water was equally available for bathing. Full spectrum lighting (6500 K) in experimental rooms was provided by T8 Activa 172 daylight tubes (Sylvania). The arrangement and nature of the sound-proof chambers prevented both visual and acoustic communication between females during our experiments (2 × 20 min per day), but outside the test period we kept the chambers open to allow females to hear each other, to avoid social isolation. The condition and health of all birds were monitored on a daily basis through observation by both experimenters and an animal caretaker and we did not detect any visible effect of isolation during the experimental period.

Before and after the experiments females were housed in social groups, several cages (118 × 50 cm and 50 cm high) being placed in a room where birds could visually and vocally interact with the individuals from other cages. The same conditions were available concerning food and water supply as well as lighting quality. To start their reproductive cycle and to synchronize periods of receptivity, the females were placed on a long-day photoperiod regime (16:8 h light:dark; Leboucher et al., 1994), after being kept

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