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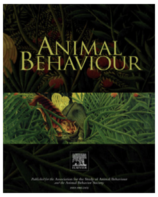

Experimental chronic noise exposure affects adult song in zebra finches

Dominique A. Potvin [a, b, *], Scott A. MacDougall-Shackleton [a, b]

[a] *Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada*
[b] *Department of Psychology, University of Western Ontario, London, ON, Canada*

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Studies over the past decade have revealed many differences in song characteristics between urban and rural populations of passerines. While some of these adjustments are immediate (i.e. flexible responses to a changing acoustic environment), there is evidence that other adjustments may occur over a longer term. We tested whether adult zebra finches, *Taeniopygia guttata*, would alter their songs after being held in different controlled acoustic environments (one quiet, one with traffic noise) for 5 months and whether these changes would (1) be associated with changes in baseline circulating corticosterone level and (2) persist 2 months after being reacclimated to their original social environment. We found that the noisy environment did not elevate baseline circulating corticosterone. In addition, although noise resulted in song changes, these changes were not consistent with the current hypotheses of acoustic masking and adaptation. Rather, we found that birds living in a noisy environment significantly lowered their minimum frequencies post-treatment, an effect that lasted at least 2 months post-experiment. Furthermore, over the course of the experiment, we found that all birds, regardless of treatment group, increased the duration of their song (by increasing the number of repeated notes within their song) and showed reduced baseline corticosterone. Our results suggest that living in different acoustic environments temporarily may have both immediate and lasting effects on song characteristics. However, because these results do not correspond with field observations of masking avoidance, we suggest that the process of song modification in different environments may be more complicated than initially hypothesized.

Studies over the past decade have reported a number of differences in song characteristics between urban and rural populations of passerine birds. Qualities of songs that appear affected by anthropogenic noise include timing in serin, *Serinus serinus*, and European robin, *Erithacus rubecula*, song (Díaz, Parra, & Gallardo, 2011; Fuller, Warren, & Gaston, 2007), meme use in house finch, *Carpodacus mexicanus*, dark-eyed junco, *Junco hyemalis thurberi*, and silvereye, *Zosterops lateralis*, song (Bermudez-Cuamatzin, Rios-Chelen, Gil, & Garcia, 2009; Cardoso & Atwell, 2011; Potvin & Parris, 2013), complexity in European robin song (Montague, Danek-Gontard, & Kunc, 2013), tempo in great tit, *Parus major*, and silvereye song (Potvin, Parris, & Mulder, 2011; Slabbekoorn & den Boer-Visser, 2006) and frequency parameters in a range of species' songs (e.g. Brumm, 2006; Francis, Ortega, & Cruz, 2011; Parris & McCarthy, 2013; Potvin et al., 2011; Slabbekoorn & den Boer-Visser, 2006). Such changes have been argued to increase the active space of song in noisy environments, especially in conjunction with increasing amplitude of the signal (Mockford, Marshall, & Dabelsteen, 2011; Nemeth & Brumm, 2010; Parris & McCarthy, 2013; Slabbekoorn, Xiao-Jing, & Halfwerk, 2012). However, the time period over which these changes take place is variable. For example, birds may be able to increase song amplitude, frequency or song type immediately in response to a change in environmental noise conditions (great tits, European robins, silvereyes and chiffchaffs, *Phylloscopus collybita*: Halfwerk & Slabbekoorn, 2009; Montague et al., 2013; Potvin & Mulder, 2013; Verzijden, Ripmeester, Ohms, Snelderwaard, & Slabbekoorn, 2010). Whether changes might occur over an individual's lifetime as a result of dispersing to a new environment, in a process similar to physiological acclimation, is a question that remains understudied in this field. Long-term, yet reversible, adjustments to a new acoustic environment may develop if a song trait is not rapidly adjustable, or if adjustments rely on a longer-term evaluation of the acoustic

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[*] Correspondence and present address: D. A. Potvin, Finnish Museum of Natural History, University of Helsinki, Helsinki, 00100, Finland.
E-mail address: dominique.potvin@helsinki.fi (D. A. Potvin).

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environment (e.g. singing an earlier dawn chorus to avoid peak traffic; Fuller et al., 2007). In addition, it is unknown whether any such song characteristics might be readjusted if the environment changes again, for example in migratory species that might encounter different acoustic environments in their wintering and breeding grounds.

Observable changes in an individual's song over a longer period may also occur as a by-product of physiological or morphological responses to the changing environment rather than reflect an attempt at increasing the active space of the song. The acoustic adaptation hypothesis predicts that vocalizations will differ between environments due to environmental selection for acoustic features that transmit well in certain habitats; for instance, an environment where background noise is concentrated at a certain frequency would select for vocalizations that avoid this frequency (masking avoidance). This hypothesis is often cited among evolutionary biologists and behavioural ecologists to explain changes in urban song. However, there has been very little investigation into how song might be affected by other processes such as physiological or behavioural impacts of a new environment. For example, urbanization can affect population density in some species of songbirds (Peris & Pescador, 2004; Valcarcel & Fernandez-Juricic, 2009), and density has been found to be a contributing factor to changes in song length in urban great tits (Hamao, Watanabe, & Mori, 2011). While many studies have focused on changes in diet, foraging behaviour, vigilance, migration, hormone levels and even susceptibility to parasites in urban birds and those subject to high levels of anthropogenic noise (Blickley et al., 2012; Bonier et al., 2007; Crino, Johnson, Blickley, Patricelli, & Breuner, 2013; Echeverría & Vassallo, 2008; Gavett & Wakeley, 1986; Partecke, Schwabl, & Gwinner, 2006; Sol, Lapiedra, & González-Lagos, 2013; Valcarcel & Fernandez-Juricic, 2009), few have attempted to understand whether and how these changes might affect song or singing behaviour. One example of such a possible connection is the finding that high levels of heavy metals in contaminated habitats affect great tit song (Gorissen, Snoeijs, Duyse, & Eens, 2005), but the mechanisms of this effect remain unknown. The lack of studies examining the mechanisms of song differences between birds living in different acoustic environments means that we do not yet fully understand what song changes might be due to a plastic adjustment with the aim of increasing the active space of a song, and what changes might be by-products of other adjustments to, or effects of, anthropogenic environments.

Another hypothesis that may explain the connection between noise and song suggests that noise may be a source of developmental or chronic stress (Wright et al., 2007). Birds living in noisy areas may chronically engage their stress response, allowing them to cope with the stressor but paying a longer-term cost. The vertebrate stress response includes increased secretion of glucocorticoid hormones (corticosterone in birds); these glucocorticoids may enhance survival in the short term by mobilizing energy, but in the long term may suppress growth and immune function and have other negative consequences (Kriengwatana, Wada, Macmillan, & MacDougall-Shackleton, 2013). Chronic stress from noise affects long-term health in many animals, including humans (Melamed & Bruhis, 1996) and poultry (Campo, Gil, & Dàvila, 2005). In addition, previous studies have found differences in stress hormone levels between birds living in noisy or urban areas and those living in quiet or rural areas (Blickley et al., 2012; Bonier et al., 2007; Crino et al., 2013; Møller, 2009; Partecke et al., 2006; Wright et al., 2007), but these effects have not yet been linked to singing behaviours.

The amount to which an individual can, or may, change its song throughout its lifetime is determined by a number of variables. First, there is a general distinction between close-ended and open-ended song learners, whereby open-ended learners learn new songs throughout their lifetime and close-ended learners develop crystallized songs or repertoires as juveniles that remain relatively unchanged during adulthood (Catchpole & Slater, 2008). Small, within-lifetime song adjustments in close-ended crystallized song are now known to be common and are often made in response to changing environmental or social conditions (Cynx, 2004; Sakata, Hampton, & Brainard, 2008; Sakata & Vehrencamp, 2012). The influence of the environment on how quickly these adjustments take place is currently unknown; however, preliminary studies suggest that stress may affect adult song consistency and stereotypy over time (Faltynek, 2014; Newman, MacDougall-Shackleton, An, Kriengwatana, & Soma, 2010). It is also unknown whether these changes might be beneficial for increasing the active space of the song in the environment, or for other functions (i.e. increased attractiveness to females; Woolley & Doupe, 2008). A second source of song plasticity is season: research on song sparrows, *Melospiza melodia*, and white-crowned sparrows, *Zonotrichia leucophrys gambelii*, has shown that song stereotypy decreases in the autumn months, and is associated with lower testosterone concentrations and smaller song control brain regions (Smith, Brenowitz, Beecher, & Wingfield, 1997; Smith, Brenowitz, Wingfield, & Baptista, 1995). These changes do not include alterations to song repertoires, and suggest that seasonal brain plasticity is associated with singing performance and song consistency in these species.

Despite the research above, it remains unclear how chronic noise exposure over a period of weeks affects birds' songs. We tested the hypothesis that zebra finches, *Taeniopygia guttata* (close-ended song learners and nonseasonal breeders), might adjust songs with lasting effects to a new acoustic environment (traffic noise) over an elongated period (5 months) in order to increase the active space of their song. Based on previous studies, these changes may include raising the minimum frequency and possibly increasing the duration of songs, as well as decreasing the tempo of songs compared to birds in quiet conditions. While it is known that zebra finches immediately increase the amplitude of their vocalizations when presented with noise (Cynx, Lewis, Tavel, & Tse, 1998), we were interested in longer-term effects of partial song masking: an ecological phenomenon common in urban and other impacted areas, and one that is biologically relevant to many species, including our focal species (Lohr, Wright, & Dooling, 2003; Swaddle & Page, 2007). We also tested whether these adjustments might be temporary or lasting by re-recording the same individuals after a post-experiment period of 2 months of being reacclimated into their normal (free of traffic noise) social environment. To establish whether any changes (adaptive or not) in song were associated with chronic stress, we also tested whether living in a noisy environment in the long term affected circulating baseline corticosterone (CORT) and whether levels of baseline CORT were correlated with any of the song attributes being measured. Long-term chronic stressors affect the hypothalamic–pituitary–adrenal axis in a variety of ways. Baseline CORT is often used as an index of individual or population health, although the relationship between this measure and fitness is variable (Bonier, Martin, Moore, & Wingfield, 2009). Although elevated baseline CORT is often used as an indicator of chronic stressors, chronic stress can sometimes result in lowered baseline CORT levels (e.g. Rich & Romero, 2005). In the present study, we predicted that if chronic exposure to traffic noise acts as a chronic stressor, then we might detect differences in baseline CORT between birds that were and were not exposed to environmental noise.