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Moving beyond species-specific noise-induced changes in birdsong: a comment on Roca et al.

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Anthropogenic (man-made) noise is a global pollutant of international concern. Although the impacts of anthropogenic noise on humans have been studied for decades (Muzet 2007), it is only in the last 10–15 years that similar attention has focused on nonhuman animals (Shannon et al. 2016). Some of the earliest work considered how vocal signalers might overcome potential masking, with research investigating changes in song frequency by birds leading the way (Slabbekoorn and Peet 2003). Studies on shifting song frequencies continue to dominate the anthropogenic-noise literature, and so the meta-analysis conducted by Roca et al. (2016), drawing together and comparing these studies, is timely and welcome.

Roca et al. (2016) demonstrate that bird species differ in whether and how they alter their song frequencies when faced with anthropogenic noise. Such interspecific variation has also been documented with respect to other behaviors (Francis et al. 2011; Voellmy et al. 2014), and is to be expected due to differences in, for instance, physiological stress responses and hearing thresholds (Hofer and East 1998; Manley 2012), as well as the variation in body size and vocal characteristics discussed by Roca et al. (2016). Because interspecific differences may alter relative success under conditions of anthropogenic disturbance, studies that start to establish which species are most at risk and if there are generalizable patterns in response are important, both for a full understanding of the impacts of anthropogenic noise and to best-inform potential mitigation measures.

Given the preponderance of such studies, Roca et al. (2016) sensibly focus their meta-analysis on birdsong (and also consider anurans). However, they rightly point out 2 extensions that are needed in this research field. First, that more work considers acoustic communication in other taxa (see also Morley et al. 2014; Radford et al. 2014). It is likely that there will be effects on the vocalizations of mammals (Parks et al. 2011), as well as the wider range of acoustic signals produced by fish (Picciulin et al. 2012) and insects (Lampe et al. 2012). Second, that there should be investigations of acoustic signals that are not sexually selected (i.e., that function in mate attraction and territory defense). Early evidence suggests that anthropogenic noise could also affect, for example, signaling about danger (Lowry et al. 2012) and communication between parents (Halfwerk et al. 2012) and between parents and offspring (Leonard and Horn 2012).

I suggest that for a complete picture of how anthropogenic noise impacts acoustic communication, 3 further elements are crucial. First, there is the need to consider not just the signaler but also the receiver. Singing at a higher pitch, for instance, is not necessarily a guarantee of success for bird species in urbanized environments (Moiron et al. 2015). Second, there should be greater consideration of the costs, as well as the potential benefits, of vocal adjustments (Read et al. 2014). Alterations in acoustic characteristics could result in many direct or indirect costs, including reduced transmission distances, increased risk of predation or parasitism, higher energy expenditure, and loss of vital information. Finally, and not unrelated to the above, fitness consequences ideally need to be assessed. Studies directly measuring how anthropogenic noise affects survival or reproductive success are rare, both with respect to acoustic communication (but see Halfwerk et al. 2011) and more generally (but see Simpson et al. 2016). However, they are ultimately required if we are to determine the consequences of this pervasive pollutant for population viability and community structure.

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A meta-analytic castle built on sand? A comment on Roca et al.

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Since Slabbekoorn and Peet (2003) first suggested songbirds sing at a higher pitch in urban noise, it has become highly fashionable to investigate this phenomenon. Output from these investigations represents the input to the meta-analysis of Roca et al. (2016). We find little to comment on regarding the design and execution of their analysis. Instead, we question whether their meta-analysis might be built on shaky ground. Here, we raise four questions pertaining to the literature on frequency shifts in anthropogenic noise in the hope that answering them will put future research on this topic on a more solid footing.

(1) Are shifts in minimum frequency an epiphenomenon of poor sound analysis practices?

In studies of noise-induced frequency shifts, it is common for researchers to use on-screen cursors to measure spectral features from spectrograms. Although this practice results in quantifiable data, it is prone to severe biases. In addition to being based on subjective cursor placements, the presence of constant background noise (e.g., anthropogenic noise) or transient high-intensity sounds (e.g., another signaling animal) can lead to measurement artifacts that yield the false impression of a positive relationship between minimum frequency and noise (Zollinger et al. 2012). Of the 36 studies that met Roca et al.'s (2016) inclusion criteria, 14 used cursor-based methods, whereas another 5 did not report how frequencies were measured. Alternative analysis methods, such as those based on the power spectrum (Zollinger et al. 2012), should be used to avoid these potentially serious confounds, lest researchers erroneously report illusory frequency shifts in anthropogenic noise.

(2) Do upward shifts in frequency represent nonfunctional byproducts of other behaviors?

At least two behavioral mechanisms explain upward frequency shifts in some bird species as a byproduct of the animals' attempts to sing louder in noise. Both mechanisms are based on the fact that song frequency and amplitude can be positively correlated. First, actively increasing vocal amplitude in noise—a common behavior in birds and mammals known as the Lombard effect—has larger effects on

extending communication distances in noise than do positively correlated increases in song frequency (Nemeth and Brumm 2010). Second, some urban songbirds preferentially sing higher-frequency elements from their repertoires that can be produced at higher amplitudes and should be less susceptible to masking (Nemeth et al. 2013). Thus, many studies of noise-induced frequency shifts, including the meta-analysis of Roca et al. (2016), potentially misplace their focus on nonfunctional byproducts of animals' attempts to improve signal-to-noise ratios by producing higher-amplitude signals.

(3) Are frequency shifts evolutionary adaptations?

Roca et al. (2016) discuss frequency shifts in terms of the acoustic adaptation hypothesis (Ey and Fischer 2009). According to this adaptationist perspective, anthropogenic noise is a form of human-induced rapid environmental change (HIREC; Sih 2013) that acts as a source of selection on signal design. But for vocal learners like songbirds, the combination of developmental and behavioral plasticity provides considerable flexibility to modify vocal frequency in the absence of evolutionary adaptation to anthropogenic noise. Even in frogs, which are not vocal learners, there is evidence for behavioral plasticity in call frequency (Bee et al. 2016). In our view, developmental plasticity and behavioral plasticity should be considered the a priori hypotheses for frequency shifts. Rapid evolutionary adaptation in response to HIREC should not be assumed, and instead should be considered a viable alternative hypothesis to be properly tested.

(4) What about receivers?

With few exceptions (e.g., Bee and Swanson 2007; Pohl et al. 2012), the literature largely ignores the question of whether anthropogenic noise actually interferes with signal reception. The tacit assumption that it does deserves greater empirical scrutiny. For example, it has been found that birds may increase their vocal frequencies in noise even when doing so yields no release from masking (reviewed in Brumm and Zollinger 2013). Small frequency shifts at high frequencies may do little to sufficiently separate signal and noise energy into different auditory filters in the nervous system. In addition, receivers may experience less masking interference than we often assume as a result of neurosensory mechanisms that give rise to spatial release from masking, dip listening, and comodulation masking release (Bee and Micheyl 2008). Such mechanisms have unexplored potential to mitigate the assumed negative impacts of anthropogenic noise.

In summary, we encourage future researchers to be more circumspect in their interpretations of putative frequency shifts by considering 1) the appropriateness of their bioacoustic analyses, 2) the possible behavioral mechanisms underlying apparent frequency shifts, 3) the likelihood of plasticity versus evolutionary adaptation to anthropogenic noise, and 4) whether observed frequency shifts actually improve signal reception.

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