



The low-frequency acoustic structure of mobbing calls differs across habitat types in three passerine families

Alexis C. Billings*

Organismal Biology, Ecology and Evolution Program, Division of Biological Sciences, University of Montana, Missoula, MT, U.S.A.

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The acoustic adaptation hypothesis predicts that animals should adaptively respond to the transmission properties of the habitat in which they communicate. Although there have been many tests of the acoustic adaptation hypothesis with birdsong, there have been very few tests with different types of bird vocalizations. Here I tested the predictions of the acoustic adaptation hypothesis with avian mobbing calls produced in closed, open and urban habitats in three families of passerine birds. I also controlled for body size and phylogeny since these are known to influence acoustic characteristics of vocalizations. I found that body size was important in duration and frequency measurements of mobbing call acoustic structure. Phylogeny explained acoustic variation in only some acoustic variables measured. I also found only the two low-frequency measurements to differ across habitats. First, 5% frequency (a measurement of low-frequency energy distribution) differed between species classified as occurring in predominately open or closed habitats, with species classified as closed having lower 5% frequency than species classified as open. This finding supports the prediction that species in closed habitats will have lower low frequencies than species in open habitats. Additionally, I found that species classified as urban had a lower minimum frequency. This is in direct opposition to the prediction of the acoustic adaptation hypothesis and previous findings for birdsong, where species appear to shift lower minimum frequencies upward, likely to avoid masking by anthropogenic noise. To confirm this finding, I also measured low frequency using power spectra with an amplitude threshold (i.e. threshold method) and confirmed the same result: species classified as urban had lower minimum frequencies than species classified as open or closed.

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Successful transmission and reception of communication signals are crucial for mate attraction, territory defence, parent–offspring relationships, behaviour synchronization and warnings about danger (Bradbury & Vehrencamp, 2011). One major challenge faced by communicating animals is that signals are corrupted and degraded as they travel through the environment (Bradbury & Vehrencamp, 2011). Therefore, the environment in which a signal is produced may have important effects on its transmission and detection.

For acoustic signals produced in terrestrial environments, there are many forms of degradation (e.g. spreading loss/acoustic impedance, reflection, refraction) and interference (e.g. masking from other sound sources) (Bradbury & Vehrencamp, 2011). How signals degrade can vary with the properties of different habitats

(Blumenrath & Dabelsteen, 2004). Therefore, the habitats in which acoustic signals evolve may select for particular signal design features. This idea was formalized by Morton (1975) as the acoustic adaptation hypothesis, which states that acoustic signals are adaptively structured to the habitat in which they are produced in order to maximize their propagation. The acoustic adaptation hypothesis was traditionally explored in natural habitats focusing on the physics of sound propagation and the transmission properties of a habitat. More recently it has also been applied to urban habitats with anthropogenic noise (Potvin, Mulder, & Parris, 2014). The acoustic adaptation hypothesis provides testable predictions of how habitat (natural or anthropogenic) may influence the structure of acoustic signals (Ey & Fischer, 2009; Roca et al., 2016).

Tests of the acoustic adaptation hypothesis have focused primarily on learned oscine birdsong (Boncoraglio & Saino, 2007; Ey & Fischer, 2009). In natural habitats, these tests have yielded mixed results: some studies have found differences in frequency, amplitude or temporal features between open and closed habitats, whereas others found no differences between habitats (reviewed in

* Correspondence and present address: A. C. Billings, School of Life Sciences, University of Nevada – Las Vegas, 4505 South Maryland Pkwy, Las Vegas, NV 89154, U.S.A.

E-mail address: alexiscbillings@gmail.com.

Ey & Fischer, 2009). In urban environments, some songbirds sing songs of longer duration (Montague, Danek-Gontard, & Kunc, 2013; Potvin & Mulder, 2013), higher amplitude (Lowry, Lill, & Wong, 2012; Templeton, Zollinger, & Brumm, 2016) or higher frequency (reviewed in Roca et al., 2016). These acoustic changes are hypothesized to increase propagation and detection in the presence of low-frequency urban noise.

Other types of bird vocalizations besides song have been less studied, but some may be well-suited signals to test the predictions of the acoustic adaptation hypothesis because some are also used for long-distance communication and rely on effective transmission with little degradation (Marler, 1955, 1957). In particular, mobbing calls are acoustic signals given by birds in response to danger. Generally, although not ubiquitously, they have a broadband acoustic structure, a loud, harsh sound and a sharp onset and termination (Marler, 1957). Like song, each species has a specific mobbing call, which functions to attract other individuals, both conspecific and heterospecific, to the location of the caller to assist in harassing and mobbing to drive the predator from the area (Pettifor, 1990). Mobbing calls are a relevant signal to test the predictions of the acoustic adaptation hypothesis for both natural and urban habitats because their structure differs widely across habitats and species (Fig. 1a), they are important for survival and thus likely experience consistent selection for optimal transmission (Potvin et al., 2014), and very few studies have explored the role of habitat in the shaping the acoustic structure of mobbing calls (Potvin et al., 2014; Proppe, Bloomfield, & Sturdy, 2010).

I tested predictions of the acoustic adaptation hypothesis for open, closed and urban habitats in mobbing calls across three families of passerine birds using a phylogenetic comparative approach (Felsenstein, 1988). I also included body size as a covariate, because body size is often found to be an important factor in acoustic vocalizations (Ryan & Brenowitz, 1985) due to larger species being able to produce lower frequencies (Fletcher, 2005).

Vocalizations produced in closed habitats are predicted to have a longer duration and lower frequencies than those produced in open habitats. Specifically, Ey and Fischer (2009) organized the predictions regarding duration and frequency of the acoustic adaptation hypothesis into six categories. Closed habitats will have: (1) longer duration, (2) lower maximum/high frequency, (3) lower minimum/low frequency, (4) lower mean frequency, (5) lower dominant frequency and (6) a narrower frequency range. These predictions between open and closed habitats are based on attenuation (inverse square law + excess attenuation; Marten & Marler, 1977) and environment-related variations, such as closed habitats may have more stable acoustic conditions than open habitats (Ey & Fischer, 2009; Morton, 1975). Lengthening the signal (prediction 1) may increase the likelihood of detection in closed habitats, whereas in open habitats, shorter signals may be less susceptible to influences from fluctuating transmission conditions (e.g. wind). Lower frequencies transmit further than high frequencies regardless of habitat. However, lower frequencies are predicted for closed habitats (predictions 2–5) because it may be more advantageous to use higher frequencies in open habitats. Wiley (2015) suggested that since reverberations are less of an issue in open habitats, individuals can use higher-frequency vocalizations in open habitats and increase the amplitude. Therefore, it is predicted that closed habitats will use lower frequencies and place more energy in the lower frequencies. Furthermore, a narrower frequency range in closed habitats (prediction 6) is predicted because the energy of the vocalization may be concentrated to certain frequencies to limit attenuation in closed habitats (Ey & Fischer, 2009; Wiley & Richards, 1978).

I tested these six predictions of the acoustic adaptation hypothesis for open versus closed habitats. I also tested one prediction

relating to urban habitats: (7) mobbing calls produced by species from urban habitats will have higher low frequencies, while controlling for both body size and phylogenetic relatedness.

METHODS

Species Selection

I selected species from three families (Corvidae, Icteridae, Turdidae) in the order Passeriformes, because these three families include species that vary in body size and are found in a wide range of habitat types. To be included in the analysis, each species had to meet the following four requirements. (1) At least two two-star or above recordings of mobbing calls were available from the Macaulay Library at Cornell's Lab of Ornithology (i.e. background noise was roughly -30 dB, with low levels of overlapping background noise, e.g. anthropogenic, river, rain, human voice, etc.). (2) Habitat information had to be available for the species. (3) Mass measurements had to be available for the species. (4) The species must be included in the phylogenetic tree of Jetz, Thomas, Joy, Hartmann, and Mooers (2012) and Jetz et al. (2014). A total of 84 species met these four requirements: 22 species from the Corvidae, 35 from the Icteridae and 27 from the Turdidae.

Acoustic Recordings

To identify the mobbing call for a species, I first examined all recordings of that species and looked for notes associated with the recording pertaining to a mobbing event (e.g. 'calls given in response to predator', 'calls given in response to approach at nest'). If notes by the recordist indicated a mobbing call, all other recordings for that species were examined for calls that sounded and looked the same. If no metadata notes existed for a recording, I assessed field guides for descriptions of a species' mobbing call, followed by searching the collection at the Macaulay Library for calls that fit the description from the field guide. About 25% of the species had more than one described mobbing call, for example Steller's jays, *Cyanocitta stelleri*, have a 'wah' and 'wek'. Both of these calls are used in the mobbing of predators and therefore have a similar function (Billings, Greene, & MacArthur-Waltz, 2017). I chose the mobbing call with the most high-quality recordings available.

Acoustic Variables

All acoustic measurements were made in Raven Pro 1.4 (Bioacoustics Research Program, 2011). All recordings were set to 44.1 kHz sampling rate and a 16-bit depth using Audacity 2.1.1.0 (Audacity®, 2015). The same spectrogram parameters were used for all analyses (window size = 15.9 ms, overlap = 75%, hop size = 3.97 ms, DFT = 4096, grid spacing = 10.8). I chose seven acoustic measurements available in Raven Pro 1.4 to test the predictions of the acoustic adaptation hypothesis (Fig. 1b): (1) delta time, the duration of the selection; (2) 95% frequency, the frequency where the summed energy exceeds 95% of the total energy in the selection; (3) low frequency (also known as minimum frequency), the lowest frequency in the selection; (4) 5% frequency, the frequency where the summed energy exceeds 5% of the total energy in the selection; (5) centre frequency (also known as mean frequency), the frequency that divides the selection into two frequency intervals of equal energy; (6) maximum/peak frequency (also known as dominant frequency), the frequency that contains the maximum energy in the selection; and (7) bandwidth 90% (a measure of frequency range), the difference between the 95% frequency and 5% frequency measurements of the selection.

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