

NOTE

Traffic Reduction during COVID-19 Lockdowns Benefited Species Already Tolerant of Noise Pollution: An Acoustic Analysis

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ABSTRACT: High levels of anthropogenic noise pollution affect wildlife globally. Traffic noise contributes a ubiquitous source of noise pollution and shows high intensity at lower sound frequencies. Animals using high-frequency sounds or broad frequency bandwidths may, to some extent, escape energetic masking by traffic noise. Although it is difficult to disentangle effects of noise pollution from those of urbanization, COVID-19 lockdowns reduced traffic in a quasi-experimental manner that isolates the effects of noise. Comparing counts of North American songbirds before and during COVID-19 lockdowns, we show that, surprisingly, species with songs more resilient to interference by noise (wider-bandwidth songs, especially) experienced more favorable changes in abundance associated with stronger reductions in traffic. Such abundance changes in human-altered landscapes during lockdowns indicate that noise pollution can be detrimental even for noise-tolerant species and that conservation of less noise-tolerant species will require more extensive limitations to anthropogenic noise than during COVID-19 lockdowns.

Keywords: noise pollution, acoustic communication, birdsong, urban ecology, COVID-19 lockdowns, demographic changes.

Introduction

Noise pollution is widespread in terrestrial environments, affecting both areas with high human densities and areas with low human densities (Barber et al. 2011). Anthropogenic noise has grown to become a concern for both hu-

man health (Mnzel et al. 2021) and biodiversity conservation (Shannon et al. 2015; Kok et al. 2023). Recognizing that noise from motorized traffic is most intense at lower sound frequencies, acoustically communicating animals that use lower sound frequencies should be more sensitive to anthropogenic noise and avoid noise-polluted areas (Francis et al. 2023). Such sensitivity is expected because of the energetic masking of vocalizations (sensu Rosa and Koper 2018; i.e., the overlap of sound frequencies between animal vocalizations and noise), which diminishes the detectability of vocalizations. Species using narrow frequency bandwidths also appear more sensitive to noise pollution than species with wide bandwidths (Cardoso et al. 2020). Since acoustic communication is vital for many animals, playing important roles in survival and reproduction, impaired detection of vocalizations is detrimental for fitness (Senzaki et al. 2020).

Although noise pollution is pervasive in urbanized landscapes (Rosa et al. 2015), lockdowns during the COVID-19 pandemic reduced noise from motorized traffic at a global scale (Bates et al. 2021; Challat et al. 2024), to the point where traffic reductions were often associated with changes in the abundances of birds (Schrimpf et al. 2021). This provided a quasi-experimental opportunity to isolate the effects of noise from confounding effects in the urban landscape (e.g., habitat destruction and fragmentation) and test which species benefit the most from noise reduction. In fact, lockdowns during the COVID-19 pandemic reduced human activity and noise pollution—a phenomenon referred

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to as an “anthropause” (Rutz et al. 2020)—to such an extent that it affected acoustic communication in wild, urban animals (e.g., Derryberry et al. 2020).

We took advantage of the COVID-19 lockdowns during 2020 to test whether frequency characteristics of bird songs were associated with changes in species counts across urban areas in Canada and the United States. Bird species with lower-frequency songs suffer more energetic masking (*sensu* Rosa and Koper 2018) by anthropogenic noise pollution, which is more intense at lower frequencies, and are therefore less likely to occupy noisy, urban environments (Hu and Cardoso 2009; Cardoso 2014). In addition, two previous investigations tested which song frequency traits predict tolerance to noise pollution among North American passerines, revealing an association between song frequency bandwidth and noise tolerance, with species with wider-bandwidth songs being more common in noisy areas (Cardoso et al. 2020; Klingbeil et al. 2020). This situation may arise because some elements of songs with broad frequency bandwidth suffer less energetic masking by noise. Additionally, songs with broad frequency bandwidth may have more extensive frequency modulation and may suffer less informational masking (*sensu* Rosa and Koper 2018) if frequency modulation makes them more dissimilar from noise pollution, which generally lacks frequency-modulated sounds, and helps cognitive processes such as attention or discrimination amid noise. Therefore, species using lower sound frequencies or narrower frequency bandwidths are expected to be more sensitive to

noise pollution than species with high-frequency or wide-bandwidth vocalizations.

If the frequency characteristics of animal sounds influence their tolerance to noise pollution, we predict that the absolute frequency or frequency bandwidth of animal sounds will correspond to the change in abundance of animals expressed in response to noise reduction during COVID-19 lockdowns. The direction of these associations, however, is difficult to predict because traffic noise was only partly reduced during COVID-19 lockdowns and did not halt completely. For partial reductions in noise pollution, it is possible that species with sounds that are more sensitive to disturbance by anthropogenic noise (i.e., low-frequency or narrow-bandwidth sounds) generally become more locally abundant because of those partial reductions of noise (gray arrows scenario in fig. 1). Conversely, species with songs that are more resilient to interference by anthropogenic noise (i.e., high frequency or broad bandwidth) may actually benefit more from partial noise reduction if noise levels still exceed thresholds that sensitive species can tolerate (black arrows scenario in fig. 1). These two alternative scenarios are plausible irrespective of how sensitivity and tolerance to noise are modeled (fig. 1).

Here we evaluate these two alternative scenarios by focusing on the songs of passerine birds, a group of animals that use long-range communication signals prone to masking by noise pollution. Given that COVID-19 lockdowns occurred between March and May in spring 2020, a time

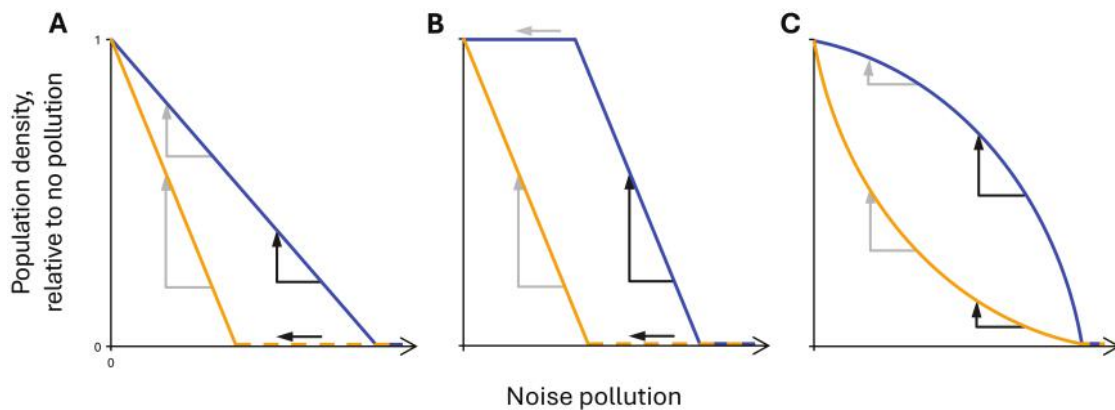


Figure 1: Graphical representation of the influence of noise pollution on population density for species that are more sensitive to noise (orange lines) versus species that are more tolerant of noise (blue lines), showing different models for these relationships. By definition, species sensitive to noise pollution will show declining population density faster (A) or sooner (B) than more tolerant species when noise pollution increases. At high levels of noise pollution, populations may subsist only because of immigration (dashed lines). These relationships may be approximately linear (A, B) or, for example, curvilinear (C). The goal of our study was to contrast the scenarios illustrated by the gray arrows versus the black arrows. It is possible that partial reductions in noise could benefit especially the more sensitive species (gray arrows scenario) or, if baseline levels of noise were high enough, especially the more tolerant species (black arrows scenario).

of year when Northern Hemisphere birds are breeding, the reduction of anthropogenic noise during lockdowns potentially stood to impact the fitness of songbirds. We studied the relationship between birdsong frequency characteristics and changes in bird counts during the anthropause of the COVID-19 lockdowns. We used data from Schrimpf et al. (2021), which showed that abundances of most bird species in Canada and the United States increased during the 2020 COVID-19 lockdowns. Reductions in traffic ranged from 8% to 25% across counties in Canada and the United States during lockdowns, and Schrimpf et al. (2021) quantified the benefit from traffic reduction for different species as the interaction term between the extent of traffic reductions and the changes in abundances before versus during lockdowns. Higher values of this interaction indicate that counts increased more in counties with larger reductions in traffic. Hereafter, we refer to this interaction effect as “traffic-related changes in abundance.” For the passerine species studied in Schrimpf et al. (2021), we measured the sound frequency and frequency bandwidth of songs and ran phylogenetic generalized least squares (PGLS) multiple regression models of traffic-related changes in abundance on song frequency and frequency bandwidth.

Material and Methods

Schrimpf et al. (2021) compared changes in abundance for 82 avian species across 93 metropolitan counties (i.e., those with >50,000 residents) in Canada and the United States between March and May of the 3 years preceding the COVID-19 pandemic (2017–2019) and between March and May during the COVID-19 lockdowns (2020), based on eBird survey data. Using a well-balanced protocol that controlled for potential effects of the pandemic on human surveying effort, eBird data were subsampled to eliminate biases due to sampling location, sampling effort, or other sampling differences between the prepandemic and pandemic periods (Sánchez-Clavijo et al. 2021). For example, to avoid bias owing to inexperienced birders (since many people may have started using eBird during lockdowns), count data from 2020 were used only from observers that had reported bird counts in the same region at some point during the previous 3 years (for further details, see Schrimpf et al. 2021). These data proved sufficiently accurate that species differences in detectability (i.e., rate at which birds provide a detectable acoustic or visual cue; Sólymos et al. 2013) did not predict demographic changes related to noise pollution (table S4 of Schrimpf et al. 2021).

For each species and county, Schrimpf et al. (2021) computed changes in abundance between the two periods (before vs. during lockdowns). They then quantified how much each species was impacted by human traffic

reduction as the interaction effect between traffic reduction in each county and the observed change in species counts from before versus during lockdown. This interaction effect evaluates demographic changes on a relative scale rather than on absolute scale and is therefore comparable among species that naturally have different population densities. Here, we refer to this interaction statistic (pandemic:delta_traf-mean from supplementary material data S3 of Schrimpf et al. 2021) as “traffic-related changes in abundance.” As in figure S10 of Schrimpf et al. (2021), we multiplied this interaction effect by -1 so that higher values of traffic-related changes in abundance indicate species that benefited more during lockdowns (i.e., counts increased more during lockdowns or showed lower reductions during lockdowns) in counties with larger reductions in traffic, compared with counties with smaller reductions in traffic.

We measured the sound frequency of songs for all passerine species included in Schrimpf et al. (2021), using song recordings from the citizen science repository xeno-canto (<http://xeno-canto.org>). Recording dates ranged from 1986 to 2023. We did not restrict the data by place, date, or habitat because our goal was to broadly characterize the among-species differences in sound frequency. For each species, we downloaded up to five recordings labeled in xeno-canto as “song” and with a sound quality rating of “A” (i.e., sounds with highest sound quality ratings). Details of acoustic measurements are provided in the supplemental PDF. Briefly, we took measurements based on amplitude differences between frequencies (peak frequency, maximum minus minimum bandwidth) and on the distribution of energy across frequencies (50th percentile frequency, interquartile bandwidth; fig. 2). The two types of sound frequency measurements, based on peak amplitude and amplitude thresholds or on energy quartiles, have different advantages. The first approach is less affected by low-amplitude background noise but uses less information from the frequency profile of songs, while the second approach uses and summarizes more of that information. For robust conclusions, we report analyses using both types of measurements. All frequency measurements were taken in $\log_{10}$ hertz, because ratio scales (i.e., log hertz) conform better to how animals perceive and modulate sound frequency (Cardoso 2013). Of the 51 passerine species in Schrimpf et al. (2021), we excluded two that do not use long-range songs and two that were outliers in the measurements of sound frequency and bandwidth (fig. S1; figs. S1, S2 are available online).

We computed the within-species repeatability of sound frequency measurements across all songs measured. We then calculated average measurements across songs in the same recording, and using these mean values per recording, we again computed within-species repeatability. To

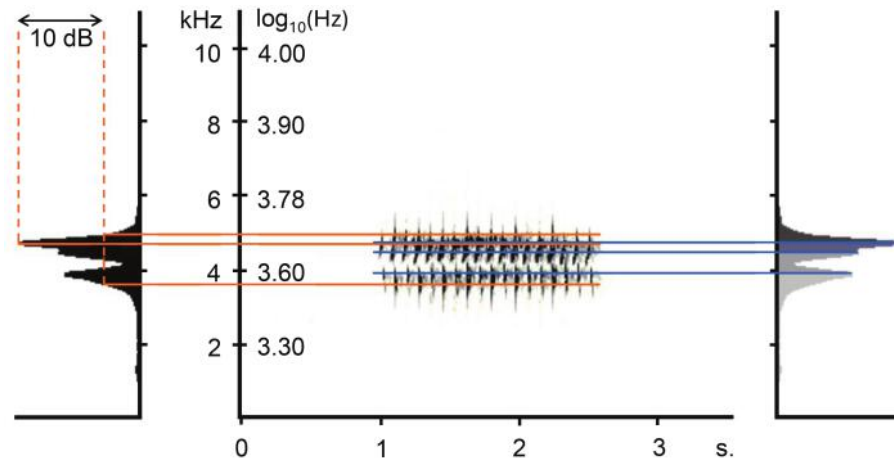


Figure 2: Sound spectrogram of a dark-eyed junco (*Junco hyemalis*) song, illustrating frequency measurements used in this study. Orange lines and the power spectrum on the left illustrate measurements of peak frequency and maximum and minimum frequencies. Blue lines illustrate measurements of the 25th, 50th, and 75th frequency percentiles, which separate the four sound energy quartiles (shown by different shades of gray in the power spectrum on the right).

compute repeatability, we used the rpt function for Gaussian data, with species identity as the grouping variable, in the R package rptR (ver. 0.9.22; Stoffel et al. 2017). Within-species repeatability was very high for peak frequency (across songs: $r = 0.82$, $P < .01$; across recordings: $r = 0.85$, $P < .01$) and 50th percentile frequency ($r = 0.88$, $P < .01$; $r = 0.88$, $P < .01$) and was also high for maximum minus minimum bandwidth ($r = 0.56$, $P < .01$; $r = 0.61$, $P < .01$) and interquartile bandwidth ($r = 0.66$, $P < .01$; $r = 0.65$, $P < .01$). These high within-species repeatability values mean that, despite potential sources of within-species variation in sound frequency (e.g., cultural learning, geographic variation, context-dependant song usage), our data characterize the species differences in the sound frequency of songs. Then using the average measurements per recording, we averaged them across recordings of the same species to obtain a single datum per trait per species for the remaining analyses.

Our dataset comprised taxonomically diverse passerine species, from 18 different families, including 32 migrant, 6 partial migrant, and 9 resident species (Tobias et al. 2022). Schrimpf et al. (2021) showed that migration affected demographic responses to the COVID-19 lockdowns, and among the 47 species in our dataset, migratory species tend to have higher-frequency songs (fig. S2). Therefore, to account for the potential confounding effect of migration, we included the migration score of each species from AVONET in statistical models (Tobias et al. 2022): 1 for sedentary, 2 for partial migrant, and 3 for migrant.

We ran a PGLS multiple regression model of traffic-related changes in abundance on song peak frequency, maximum minus minimum bandwidth, and migration

score. We ran another PGLS model of traffic-related changes in abundance on 50th percentile frequency, interquartile bandwidth, and migration score. We did not include body size in these models because size is strongly related to sound frequency across passerine birds (and less so to frequency bandwidth; Friis et al. 2021), and Schrimpf et al. (2021) showed that body size did not influence abundance changes in relation to human activities. We ran PGLS regressions while estimating model λ to adjust the phylogenetic correction to the degree of phylogenetic signal in the model (Freckleton et al. 2002). To account for phylogenetic uncertainty, we ran PGLS regressions based on 1,000 ultrametric trees (Rubolini et al. 2015), downloaded from <http://birdtree.org> (Jetz et al. 2012) with the Hackett (2008) tree backbone, and performed model averaging weighed by Akaike's weights (Garamszegi and Mundry 2014; Piccoli et al. 2025). We report model averages of model λ and of the standardized partial regression coefficient for each predictor (β_{st}) and computed their associated P values. We ran PGLS analyses with the R package caper (ver. 1.0.3; Orme et al. 2023).

Results and Discussion

During COVID-19 lockdowns, traffic-related changes in abundance were positive for some bird species, meaning that these species benefited more (i.e. species counts increased more or decreased less) in counties with larger reductions in traffic (fig. 3A–3D). Other species benefited more in counties with lower reductions in traffic (fig. 3A–3D). This is consistent with Schrimpf et al. (2021), which showed wide differences between species in responses

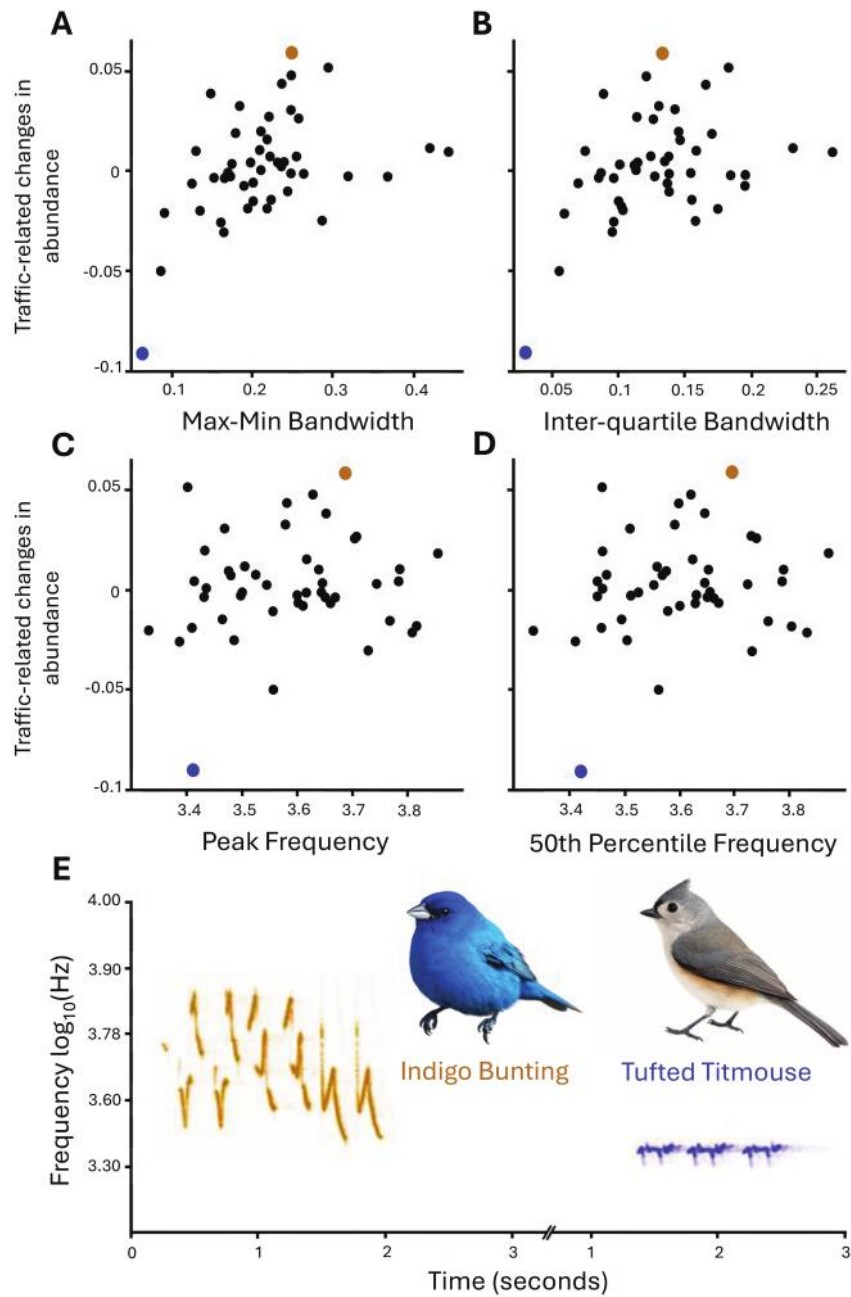


Figure 3: Traffic-related changes in abundance during the COVID-19 lockdowns for 47 species of North American songbirds, in relation to the sound frequency of their songs. Higher values indicate species that benefited more with traffic reduction (i.e., counts increased more, or were less reduced, in counties with larger reductions in traffic). Passerine birds showed a positive relationship between traffic-related changes in abundance and the frequency bandwidth of their songs (A, B) and, to a lesser extent, also a positive relationship between traffic-related changes in abundance and their absolute song frequency (C, D). E shows sound spectrograms of representative songs for the species with the highest (orange) and lowest (blue) benefits from traffic reductions.

to changes in traffic. As shown by Francis et al. (2009), advantages due to persisting noise pollution may exist for some species if noise is detrimental to their predators or to their competitors.

Focusing on how the sound frequency traits of song in different passerine species predicted traffic-related changes in abundance, we found that, on average, species using wider frequency bandwidths had higher scores than species using narrower bandwidths (partial β_{st} for maximum minus minimum bandwidth = 0.45, $P = .002$; partial β_{st} for interquartile bandwidth = 0.45, $P = .001$; fig. 3A, 3B). This means that they benefited more from traffic reductions during COVID-19 lockdowns. To a lesser extent, species using higher absolute frequencies also had higher scores for traffic-related changes in abundance than species using lower frequencies, although these associations were not significant (partial β_{st} for peak frequency = 0.20, $P = .18$; partial β_{st} for 50th percentile frequency = 0.20, $P = .17$; fig. 3C, 3D). In line with Schrimpf et al. (2021), the association between migration and traffic-related changes in abundance was positive, suggesting that migratory species benefit more from traffic reduction, but here this effect was not significant (partial β_{st} for migration in first model = 0.13, $P = .28$, model $\lambda = 0.02$; partial β_{st} for migration in second model = 0.18, $P = .11$, model $\lambda < 0.01$).

Both wide frequency bandwidth and high sound frequency should give birdsongs some resilience to anthropogenic noise, but previous work with North American passerines indicated that it is especially the wider-bandwidth species that better tolerate noise pollution (Cardoso et al. 2020). This may explain why we found that frequency bandwidth was a stronger predictor of traffic-related changes in abundance than the absolute frequency of songs. Our results indicated that the species benefiting most from traffic reduction were those with songs potentially more resilient to anthropogenic noise (wider-bandwidth songs and, to a lesser extent, perhaps higher-frequency songs), implying that prelockdown levels of noise pollution were often detrimental even for those more noise-tolerant species. This is consistent with previous findings that although species with songs less masked by noise are more likely to tolerate urban environments, they still do not prefer urban over natural environments (reviewed in Cardoso et al. 2018).

If noise pollution had been completely suppressed, over a time period sufficient for population numbers to readjust, then, in contrast to our results, we would have predicted that noise-sensitive species should exhibit higher values of traffic-related changes in abundance than noise-tolerant species. This is because noise-sensitive species suffer greater effects from noise pollution (Francis et al. 2011) and therefore have the greatest potential to recover

in the absence of noise. For example, for animal species that are more sensitive to noise, increasing noise pollution may induce faster decreases in fitness and abundance (orange lines in fig. 1A), or fitness and abundance may start declining at lower levels of noise (orange lines in fig. 1B), compared with more tolerant species (blue lines in fig. 1A, 1B). Population decline may also happen nonlinearly as noise pollution increases, with more severe effects for more sensitive species (e.g., fig. 1C). Regardless of how sensitivity to noise is modeled (fig. 1), complete suppression of noise would facilitate more recovery for sensitive species compared with tolerant species.

However, anthropogenic activities and noise pollution were only partly suppressed during COVID-19 lockdowns, and as a consequence, other outcomes are possible. Regardless of how we model sensitivity to noise (e.g., fig. 1), partially alleviating noise pollution is expected to primarily benefit the most noise-sensitive species only for certain ranges of change in noise intensities (gray arrows scenario in fig. 1) but not others (black arrows scenario in fig. 1). It is also possible that, for high intensities of noise pollution, partial alleviation of noise mostly benefits the more tolerant species. This latter scenario arises when levels of noise pollution are much higher than what the more sensitive species tolerate, and therefore partial alleviation is insufficient for those species to recover (black arrows in fig. 1). Our results are consistent with the latter scenario, whereby noise pollution was often sufficiently high that traffic reductions of 8%–25% (Schrimpf et al. 2021) were insufficient for more sensitive species to recover to the same degree as more tolerant species. This scenario is unsurprising, since we analyzed bird populations from counties with large metropolitan areas (>50,000 human residents), and given the extent of infrastructure and ubiquity of anthropogenic noise in North America (e.g., Barber et al. 2011).

Species with songs more resilient to noise pollution may have been able to increase their counts during COVID-19 lockdowns because they cope better with persistent traffic noise or because they were already present in noise-polluted areas and could therefore quickly benefit from changes in the environment. Species with songs more sensitive to noise did not show as great a benefit of noise reduction. Either the intensity of noise reduction or the duration of lockdowns (multiple months in spring 2020) could have been insufficient for these more noise-sensitive species to increase population densities. Additionally, the recovery of more noise-resilient species when traffic levels decreased might in some cases have negatively impacted more noise-sensitive species via competition (Francis et al. 2009).

Our results, indicating that the songbirds benefiting more from traffic reduction were those using a range of sound frequencies more resilient to interference by traffic

noise, highlight the need for not only alleviating noise but also preserving regions without noise pollution to protect the diversity of acoustically communicating animals, including noise-sensitive species. While noise reduction during COVID-19 lockdowns temporarily benefited many wildlife species, more permanent solutions, such as using quieter electric vehicles and increased funding for public transportation, are necessary to reduce effects of this pervasive pollutant.

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Statement of Authorship

P.M.S. conducted the research, collected and analyzed data, and wrote the original draft. D.J.M. supervised the research. N.K. provided data. G.C.C. proposed the study and supervised the research. All authors contributed ideas and revised the original draft.

Data and Code Availability

The data and code for the results presented here are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.18302662>; Santos et al. 2026).

Literature Cited

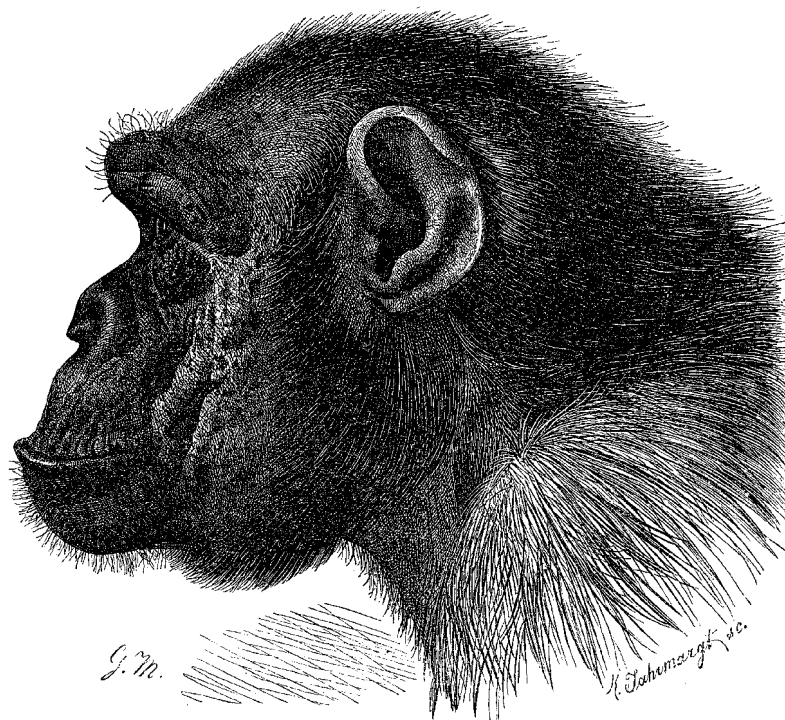
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“Then succeeds a more special account of the gorilla, the chimpanzee, and the tschego (*Anthropopithecus tschego*) [figured], and orang.”
From the review of Brehm’s *Animal Life* (*The American Naturalist*, 1877, 11:557–559).