PANDEMIC PAUSE

Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown

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Actions taken to control the coronavirus disease 2019 (COVID-19) pandemic have conspicuously reduced motor vehicle traffic, potentially alleviating auditory pressures on animals that rely on sound for survival and reproduction. Here, by comparing soundscapes and songs across the San Francisco Bay Area before and during the recent statewide shutdown, we evaluated whether a common songbird responsively exploited newly emptied acoustic space. We show that noise levels in urban areas were substantially lower during the shutdown, characteristic of traffic in the mid-1950s. We also show that birds responded by producing higher performance songs at lower amplitudes, effectively maximizing communication distance and salience. These findings illustrate that behavioral traits can change rapidly in response to newly favorable conditions, indicating an inherent resilience to long-standing anthropogenic pressures such as noise pollution.

Actions taken to mitigate the threats of coronavirus disease 2019 (COVID-19) to human life and welfare have inadvertently resulted in a natural experiment offering unanticipated insight into how human behavior affects animal behavior (*1*). Worldwide, elective quarantine and stay-at-home orders have reduced the use of public spaces and transportation networks, especially in cities. Anecdotal media accounts suggest that restricted movement has elicited rarely observed behaviors in commensal and peri-urban animals (*2*). Although not all of the reports have proven to be accurate (*3*), widely publicized observations such as coyotes crossing the normally heavily trafficked Golden Gate Bridge in the San Francisco Bay Area have provoked widespread fascination with the prospect that animals rapidly move back into landscapes recently vacated by humans.

Reports also indicate that animals have been exploiting newly emptied soundscapes. Media outlets have noted people becoming newly aware of more conspicuous animal sounds such as bird songs, particularly in normally noisy areas (*4*). Although people staying at home may simply be paying closer attention to the animals around them, it is possible that restricted human movement has reduced the use of motorized vehicles, effectively unmasking bird songs otherwise obscured by the associated noise pollution. Theory also suggests that animals should respond to reduced background noise by altering their acoustic signals to optimize the transmission of information (*5*, *6*). Resolving this uncertainty presents an unprecedented opportunity to address enduring questions about how human behavior alters soundscapes and animal acoustic behaviors (*7*) while offering vital insight into biotic resilience to long-standing anthropogenic pressures.

Our prior work on soundscapes and bird song across the San Francisco Bay Area provides a strong predictive framework for testing the hypothesis that birds altered their acoustic signaling in response to reduced noise pollution during the recent statewide COVID-19 shutdown. We quantified variation in the soundscape across urban areas (San Francisco and Contra Costa County; hereafter, simply "urban") and nearby, more rural areas (Marin County; hereafter, simply "rural"; Fig. 1A), focusing on breeding territories of white-crowned sparrows (*Zonotrichia leucophrys*; Fig. 1B), a common songbird in the area (*8*). We also characterized songs produced by males at a subset of sites within urban and rural areas, circumscribing four independent song populations known as dialects (Fig. 1C and fig. S1). Prepandemic data collected in April to June of 2015 and 2016 were compared with parallel data derived from recordings made at the same sites in April and May of 2020 (i.e., shortly after the execution of regional and statewide shelter-at-home mandates). To provide further context, we have drawn additional comparisons with data collected from the same urban and rural areas in prior decades, leveraging long-term studies of white-crowned sparrow song in the region (*9*). This approach enabled us to determine (i) whether movement restriction resulted in a soundscape with lower anthropogenic noise levels and (ii) if birds responded by adjusting their communication behaviors to improve signal transmission (i.e., efficacy) and functional signal value (i.e., salience).

We have previously shown that white-crowned sparrow songs vary predictably according to transmission properties of urban and rural soundscapes around the San Francisco Bay Area (*9*, *10*). Although urban and rural areas both exhibit spatial variation in noise levels (*10*), urban soundscapes exhibit more sound energy, particularly at low frequencies, which occurs with greater traffic flow. Birds holding breeding territories in areas with higher noise levels sing higher-amplitude songs (*11*), a common response to noise known as the Lombard effect (*12*). Males also produce songs with higher minimum frequencies (*13*) in areas with high-energy, low-frequency noise typical of traffic in cities (*10*). Consistent with signal detection theory, this improves signal efficacy by increasing communication distance (*6*), but it can come at a cost (*14*). Males that sing at higher minimum frequency often have lower vocal performance (*15*), which here is the ability to produce rapid trills at wide frequency bandwidths (Fig. 1, D and E) (*16*). Songs of males with lower vocal performance are less salient in male-male competitive interactions that occur when males defend territories (*17*, *18*). Accordingly, if noise levels decline, then males should produce songs at lower amplitudes (*19*) and lower minimum frequencies (*20*), thereby increasing communication distance while also allowing for higher vocal performance.

Comparison of recordings before and during the recent COVID-19 shutdown demonstrated that movement restriction resulted in significantly lower noise levels across more urban areas of the study region, effectively reversing more than a half-century rise in noise pollution (Fig. 2). This is well illustrated in comparisons of background noise (LAF90: the maximum noise level experienced ≥90% of the time), which is biologically relevant to songbirds and humans (*21*). Before the shutdown, breeding territories of urban white-crowned sparrows were on average nearly three times as loud as rural territories ($\beta = 9.2$ dB ± 2.1; $t_{10} = 4.4$, $P < 0.002$, where 9.5 dB is a tripling of sound pressure levels; Fig. 2A and table S1). During the shutdown, background noise was substantially lower across urban territories ($\beta = -7$ dB ± 0.8; $t_{457} = -8.8$, $P < 0.0001$) but not so across rural territories ($\beta = -1.4$ dB ± 0.9; $t_{457} = -1.6$, $P < 0.11$). This is consistent with the observation that traffic is a primary source of background noise across urban San Francisco, whereas the ocean and wind generate background noise in nearby rural Marin County (*10*). Notably, urban territories no longer exhibited higher noise levels than rural territories ($\beta = 3.6$ dB ± 2.2; $t_{10} = 1.7$, $P < 0.13$). The

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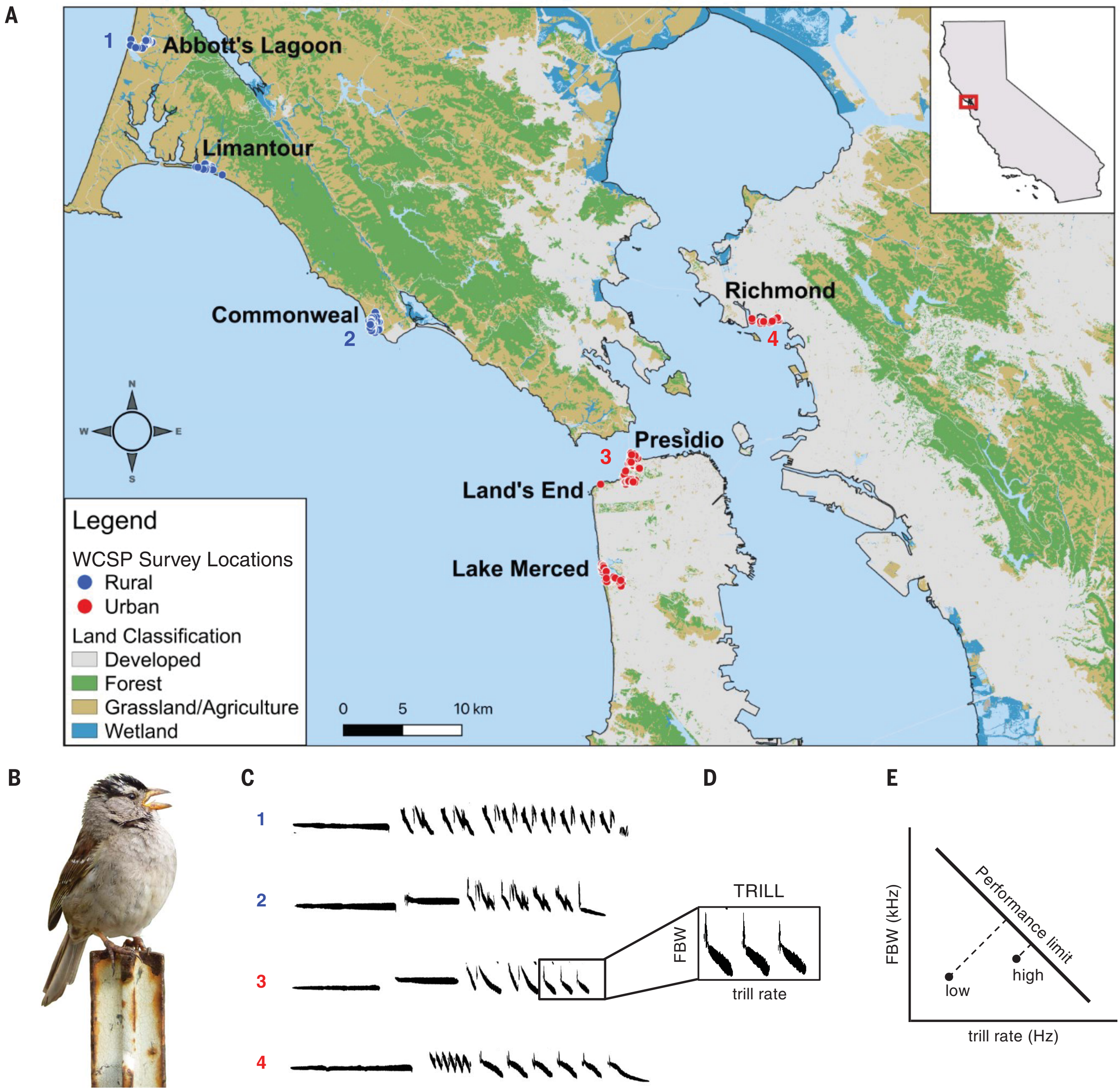

Fig. 1. Study system and song traits of interest. (**A**) Map illustrating locations where noise was recorded in urban areas (red; Presidio, Land's End, and Lake Merced) of San Francisco (San Francisco County) and Richmond (Contra Costa County), as well as in nearby, more rural areas [blue; Abbott's Lagoon, Limantour, and Commonweal (Marin County)] before (2016) and during (2020) the recent statewide COVID-19 shutdown. Numbers 1 to 4 denote locations where songs were also recorded. (**B**) Photograph of a male white-crowned sparrow (*Z. leucophrys*) singing in his territory (photo by J.N.P.). (**C**) Spectrograms of the four song dialects: (1) Drake, (2) Clear, (3) San Francisco, and (4) Berkeley, with numbers corresponding to their respective occurrence at sampling locations depicted in (A). (**D**) Trilled portion of song boxed on San Francisco dialect to illustrate measurements of trill rate (number of notes/s) and frequency bandwidth (FBW; i.e., the difference between trill maximum and minimum frequency). (**E**) Males face a physiological limit on producing fast trills at wide frequency bandwidths, resulting in a triangular distribution of songs with an upper bound performance limit. Songs closer to the limit are denoted "high" vocal performance compared with songs further from the limit ("low").

spectral profile of noise on urban territories also converged on that of rural territories (Fig. 2B). The inference that the observed shifts are due to a reduction in the high-energy, low-frequency sound generated by motor vehicles is supported by traffic flow data from the Golden Gate Bridge. Although vehicle crossings have progressively increased since the bridge opened in 1937, vehicle crossings in April and May of 2020 returned to levels not seen since 1954 (Fig. 2C). Although noise recordings are not available from the 1950s, this benchmark indicates that the relatively brief but large changes in human behavior effectively erased more than a half-century of urban

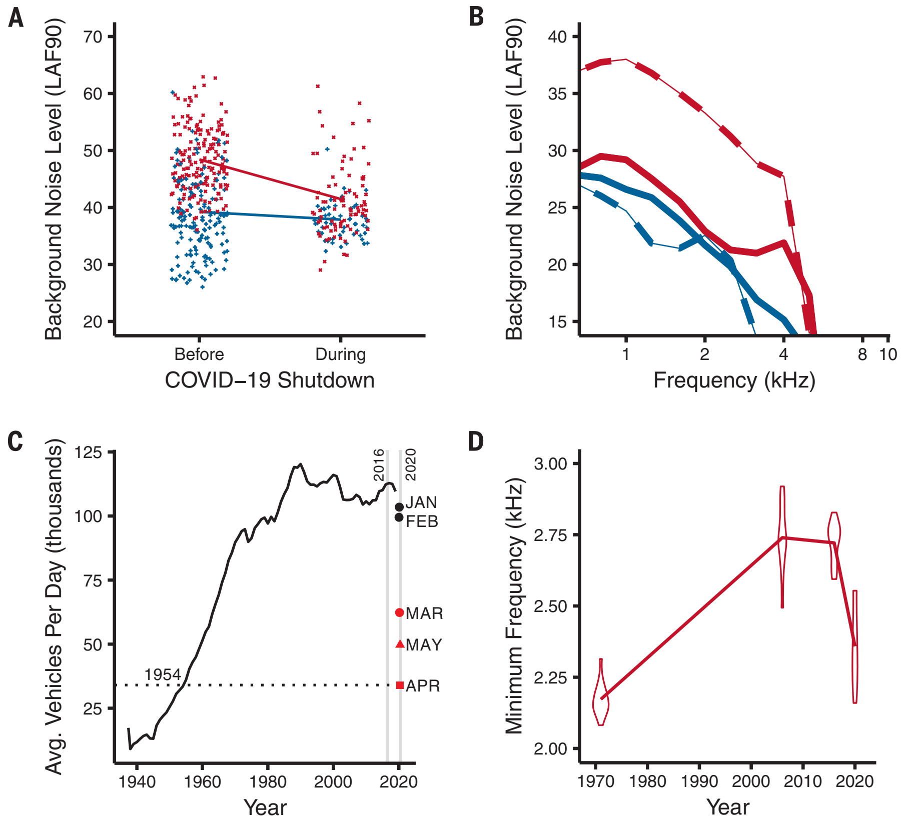

Fig. 2. Background noise levels. (**A**) Background noise levels recorded in urban (red) and rural (blue) areas, with regression lines representing model-predicted changes in background noise levels before (2016) versus during (2020) the COVID-19 shutdown. (**B**) Power spectra of background noise levels recorded before (dashed lines) versus during (solid lines) the shutdown. Urban soundscapes during the shutdown converge on the spectral profile of rural soundscapes (note that solid lines are closer together than dashed lines). (**C**) Toll data showing traffic flow on the Golden Gate Bridge in San Francisco between 1937 and 2020. Vertical gray bars mark the years before (2016) and during (2020) the shutdown, when background noise levels were recorded to illustrate the concurrent decline in the average number of vehicles crossing the bridge per day in March to May 2020, returning to levels not seen since the 1950s in April (dashed line). (**D**) Violin plots of trill minimum frequency for the Berkeley song dialect recorded in Richmond in 1971, 2006, 2016, and 2020. Line connects the mean for each time point.

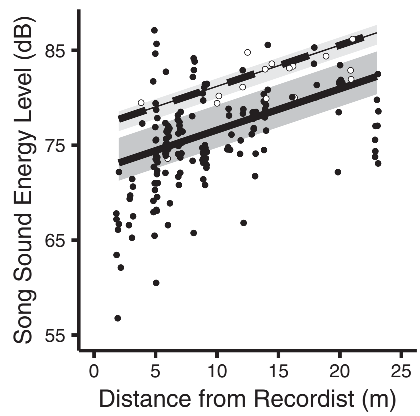

Fig. 3. Scatterplot of song amplitude versus distance between the recordist and bird. Regression lines represent model-predicted changes in song energy levels for songs recorded before (open circles, dashed line) versus during (closed circles, solid line) the COVID-19 shutdown from a slice of immediate ambient noise conditions (43 to 53 dB). The full range of noise levels is illustrated in fig. S3. Gray regions illustrate the middle 50% of the bird random effect (i.e., individual variation).

noise pollution and the concomitant soundscape divergence between urban and nearby rural areas. In other words, the COVID-19 shutdown created a proverbial "silent spring" across the San Francisco Bay Area.

Movement restriction also resulted in significantly lower ambient noise levels (LAeq), which correspond to the short-term, loud events occurring ≤10% of the time (e.g., planes flying overhead or dogs barking). Both urban and rural territories exhibited significantly lower ambient noise levels during the COVID-19 shutdown (urban: $\beta = -7.4$ dB ± 0.74; $t_{466} = -10$, $P < 0.00001$; rural: $\beta = -3.6$ dB ± 0.8; $t_{466} = -4.5$, $P < 0.00001$; fig. S2 and table S2). The drop in ambient noise levels in urban areas was greater than that in rural areas, again resulting in urban territory noise levels converging on those of rural territories.

We found clear evidence that birds responded to the reduction in noise pollution during the COVID-19 shutdown. Consistent with prior studies (*11*, *22*), we found that birds sang more softly when noise levels were lower ($\beta = 0.27$ dB ± 0.04; $t_{281} = 7.0$, $P < 0.0001$), i.e., the Lombard effect, and at shorter recording distances ($\beta = 0.43$ dB/m ± 0.08; $t_{281} = 5.3$, $P < 0.0001$) before and during the shutdown. Notably, birds produced songs at even lower amplitudes during the shutdown ($\beta = -4.08$ dB ± 1.4; $t_{87} = -3$, $P < 0.004$; Fig. 3, fig. S3, and table S3), well beyond what would be expected from the Lombard effect alone. This departure reveals that prevailing theories of animal communication do not capture the potential magnitude of vocal responses to noise abatement beyond the Lombard effect. Despite a reduction in song amplitude, communication distance more than doubled during the shutdown ($\beta = 8.4$ dB ± 1.9; $t_{87} = 4.4$, $P < 0.0001$; fig. S4 and table S4), further indicating the impact of noise pollution on communication during normal conditions.

This doubling in communication distance could elevate fitness by reducing territorial conflicts (*23*) and increasing mating potential. In addition, the signal-to-noise ratio doubled in relative energy ($\beta = 6.5$ dB ± 2; $t_{95} = 3.3$, $P < 0.002$; table S5), which helps to explain media reports suggesting that bird songs sounded louder during the shutdown (*4*). A doubling would allow people to hear birds at twice the previous distance, or effectively four times more birds than usual (*21*).

Birds also exhibited greater vocal performance in response to being released from masking by high-energy, low-frequency noise. We found that birds sang at lower minimum frequencies, achieving greater bandwidth songs in newly open acoustic space (Fig. 4 and tables S6 to S10). An increase in frequency bandwidth results in the transmission of more information and greater vocal performance. Greater vocal performance could also have been achieved through an increase in trill rate, but temporal features of song are not predicted to change with acoustic noise levels. Consistent with this prediction, we found no change in trill rate (top model = null model). Observed changes in performance and related song attributes were much greater in urban than in rural areas, which corresponds to a greater decline in noise levels in urban areas. For example, songs in urban areas exhibited a fourfold greater decrease in minimum frequency ($\beta = -162$ Hz ± 26; $t_{181} = -6.3$, $P < 0.00001$; Fig. 4A) compared with songs in rural areas ($\beta = -40$ Hz ± 35; $t_{181} = -1.2$, $P < 0.26$). This translated into a substantially greater increase in vocal performance in urban songs (β = 11.1 ± 0.6; t_{181} = 17.3, P < 0.00001; Fig. 4C) compared with rural songs (β = 2.1 ± 0.8; t_{181} = 2.5, P < 0.02). As suggested by our prior experiments (*13*, *15*, *17*, *18*), the 11-point increase in vocal performance observed in urban areas far exceeds the four-point threshold of change that results in significantly greater signal salience during male-male competition in white-crowned sparrows (*17*, *18*).

Because the same individuals were not sampled at each time point [the mean longevity of white-crowned sparrows is 13 months (*24*)], we cannot determine whether the observed shift in vocal performance was due to immediate flexibility (*25*) or if it was because males with higher performance (but typically more masked) songs outcompeted males with lower performance (but less masked) songs for breeding territories during the COVID-19 shutdown. It is nonetheless possible to infer that, on average, birds in urban areas exhibited much greater capacity to compete for breeding territories. This highlights the intriguing possibility that more juveniles preferentially copied higher performance songs during the shutdown. If so, then the shutdown may have altered the trajectory of cultural evolution within and among populations in the study region. Reevaluating the same birds after the resumption of human activity would clarify what behavior(s) gave rise to the observed population-level shift in vocal performance and potential evolutionary outcomes of the COVID-19 shutdown.

Like the half-century soundscape reversion that occurred in more urban areas of the study region, some bird songs exhibited traits during the shutdown that have not been heard in decades, such as trill minimum frequency (fig. S5). Comparisons of historical recordings illustrate that minimum frequencies have tracked a progressive half-century rise in background noise levels in urban songs. Notably, at the Richmond site in Contra Costa County (Fig. 1), the minimum frequency of the Berkeley dialect recorded during the COVID-19 shutdown approached lows not recorded since the spring of 1971 (Fig. 2D) (*26*).

Although it is well understood that noise pollution can constrain and alter animal communication (*7*, *19*, *20*), we show here that alleviation of acoustic pressures can elicit rapid responses that increase acoustic signal efficacy and salience (*14*). Our findings indicate that songbirds such as white-crowned sparrows have an outstanding capacity to exploit newly empty soundscapes after acute but ephemeral amelioration of noise pollution, suggesting that lasting remediation might engender even more promising outcomes such as demographic recovery and higher species diversity (*27*) in urban areas. Our findings also show that rapid recovery is possible despite long-standing legacies of chronic exposure, akin to responses that have been observed after the cessation of chemical pollution that persists in the environment (*28*). Determining the pace and tempo of responses to the resurgence of noise pollution after the resumption of human activity would help to shed further light on behavioral resilience. It would also afford opportunities to understand broader dynamics arising from movement restriction, including the possibility that elevated threats to animal welfare lead to complex trade-offs (*29*). Similarly minded assessments of organismal responses to the amelioration of other forms of pollution during the COVID-19 shutdown, such as reduced CO_2 emissions (*30*), would also provide exciting opportunities to develop a more integrated understanding of how animals respond to reduced human activity (*1*), including how and why animals move back into otherwise occupied landscapes and soundscapes.

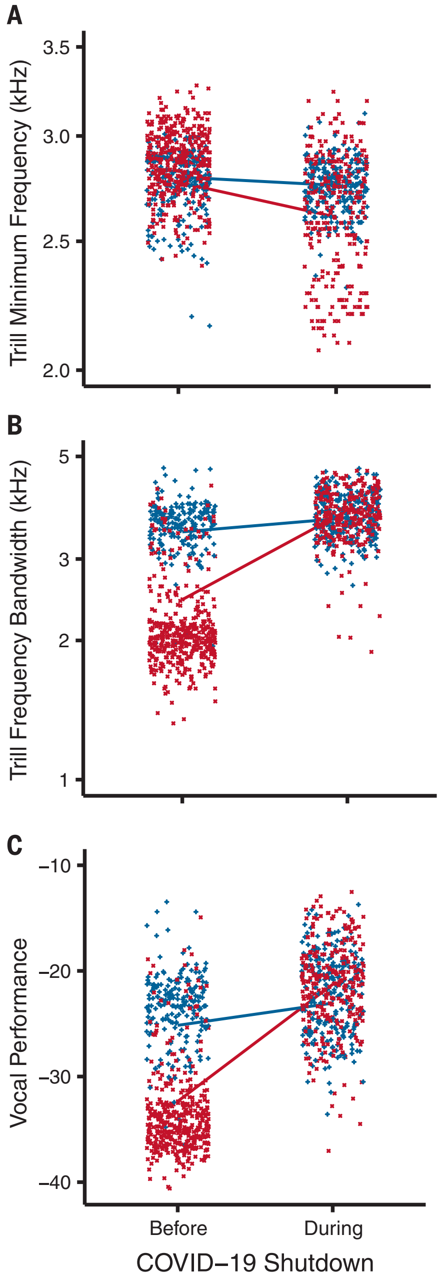

Fig. 4. Scatterplots of raw data. Shown are data recorded in urban (red) and rural (blue) areas, with regression lines representing model-predicted changes in traits before versus during the recent statewide COVID-19 shutdown for trill (**A**) minimum frequency, (**B**) frequency bandwidth, and (**C**) vocal performance. Frequency measures were plotted on a log scale because pitch perception functions on a log scale.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S4
Tables S1 to S10
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MDAR Reproducibility Checklist

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Songbirds reclaim favored frequencies

When severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) pandemic lockdowns were instituted across entire countries, human activities ceased in an unprecedented way. Derryberry *et al.* found that the reduction in traffic sound in the San Francisco Bay Area of California to levels not seen for half a century led to a shift in song frequency in white-crowned sparrows (see the Perspective by Halfwerk). This shift was especially notable because the frequency of human-produced traffic noise occurs within a range that interferes with the highest performance and most effective song. Thus, our "quiet" allowed the birds to quickly fill the most effective song space.

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