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Background noise but not urbanization level impacted song frequencies in an urban songbird in the Pearl River Delta, Southern China

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ABSTRACT

Rapid urbanization has profoundly transformed habitats and increased noise pollution in urban environments. Elevated noise levels may mask acoustic signals of urban-dwelling organisms such as birds. Singing at higher frequencies is one of typical responses to avoid this masking effect. However, high-frequency signals experience larger attenuation when transmitting in open urban environments. Here, we tested how elevated noise and urbanization affect frequency characteristics and song complexity in the Oriental Magpie-robin (*Copsychus saularis*), a common urban songbird in tropical Asia. Song recording was conducted in seven cities in the Pearl River Delta, southern China, a highly developed region with rapid pace of urbanization. Our results showed that Magpie-robins sang with higher minimum and maximum frequencies in noisier areas. Neither noise level nor urbanization level impacted other song features, including song length, syllable rate, number of syllables, number of unique syllable types, and syllable transitions in songs. Furthermore, noise level did not affect the choice of song post sites. Our results imply elevated noise levels could induce spectral but not temporal and structural modifications. Taken together, our study adds to a growing number of publications illustrating how phenotypes of birdsongs have been changed in anthropogenic soundscapes.

1. Introduction

Rapid urbanization has occurred in China in the past three decades, with nearly two-thirds of the country's population now living in cities (Yu et al., 2020). Urbanization profoundly alters landscapes and acoustic soundscapes by replacing rural and natural habitats with anthropogenic structures and impervious surfaces and through the introduction of anthropogenic noise sources such as automobile traffic and machinery (Seto et al., 2012; Warren et al., 2006). These alterations challenge acoustic communication among urban organisms, particularly songbirds who use vocal signals (songs) for important fitness-related functions such as territory defense and mate attraction (Halfwerk and Slabbekoorn, 2013; Luther et al., 2016; Slabbekoorn and Ripmeester, 2008). To better plan and manage artificial landscapes in order to support biodiversity in urban environments, it is crucial to understand the impacts of

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urbanization on animal communication and fitness under increasing levels of background noise (Richards and Wiley, 1980; Warren et al., 2006; Wiley and Richards, 1982).

Song transmission is impacted both by background noise levels and the physical environments where the songs are produced. Background noise in the same frequency range as a bird's song could lead to masking effects, resulting in reduced signal efficiency (Slabbekoorn and Ripmeester, 2008). Noise masking could lead to delayed intruder detection and defense responses, increasing defense costs for territorial males (Grabarczyk and Gill, 2019; Kleist et al., 2016; Zwart et al., 2016). High levels of background noise may also constrain the active space of advertising signals and hamper mate attraction (Bee and Swanson, 2007). In addition to elevated noise levels, the physical environmental structure in urban habitats (e.g. building facades and concrete road surfaces) can cause reverberations, signal scattering, and excess attenuation (i.e., reduction of signal intensity or purity) (Warren et al., 2006; Yip et al., 2017). Signals have been found to degrade more in urban habitats due to greater attenuation and reverberation, especially for higher frequency signals (above 5 kHz and 2 kHz, respectively) (Phillips et al., 2020).

Behavioral plasticity enables individuals to rapidly respond to signal impacts caused by elevated noise and urbanization levels (Gross et al., 2010). Birds modify their songs to maximize transmission efficiency in response to these environmental impacts (Gil and Brumm, 2014; Nemeth et al., 2013). Since urban noise is typically loudest in the range between 1 and 2 kHz (Lohr et al., 2003; Wood and Yezerinac, 2006), one commonly documented response to urban noise is an upward shift of song frequencies which could alleviate the masking effect (Fernández-Juricic et al., 2005; Halfwerk and Slabbekoorn, 2009; Lee and Park, 2019; Phillips et al., 2020; Slabbekoorn and Peet, 2003; Wood and Yezerinac, 2006). Species that sing with intermediate minimum frequencies (between 1 kHz and 1.5 kHz) are more likely to increase the signal frequency of their vocalizations in response to noise masking (Hu and Cardoso, 2010; Parris and McCarthy, 2013). However, there are potential costs associated with singing at higher frequencies. For example, reverberations and attenuation are greater for higher frequencies (Boncoraglio and Saino, 2007; Morton, 1975; Phillips et al., 2020) and so in the absence of noise, birds might be predicted to reduce the maximum frequency of their songs in densely urbanized habitats (Slabbekoorn et al., 2007). Therefore, there may be a tradeoff in dense urban areas impacting the benefits of singing with higher frequencies to avoid signal masking.

Besides spectral modifications, other song features (temporal and structural) are expected to change due to noise and urbanization. For example, song length, measured as the duration from the first syllable to the last one within one song, may vary to increase the detection under noisy conditions (Hamao et al., 2011; Nolan and Hill, 2004), however, song length showed species-specific responses to noise (Fernández-Juricic et al., 2005; Hamao et al., 2011; Ríos-Chelén et al., 2015, 2013). Moreover, though fast songs with short inter-elements are expected in habitats with simple vegetation, slow songs with lower syllable rates were found in noisy urban habitats, probably due to longer inter-syllable intervals (Potvin et al., 2011). The impacts of noise and urbanization on song structural features also showed inconsistent results. The most common studied structural feature is song complexity (without standardized definition). Various estimations of song complexity lead to confusion in comparison among studies among different species (Benedict and Najar, 2019; Soma and Garamszegi, 2011). An increase of minimum frequency due to urban noise could even constrain the elaboration of song complexity (quantified as the number of unique syllable types within a song) when testing European robins (*Erithacus rubecula*) in noise-exposure experiments (Montague et al., 2013). This was concluded as the result of plasticity integration (i.e., the plasticity of one trait may affect the expression of other potentially correlated traits) (Schlichting, 1989). Yet, song complexity (quantified as the number of syllables per song, the number of unique syllable types per song and the number of transitions between syllable types per song) showed no significant variations along the gradient of urbanization in testing Oriental Magpie-robin (*Copsychus saularis*) across seven Asian countries (Hill et al., 2018; Sasahara et al., 2012). Though low-frequency syllable types may be eliminated to avoid noise masking, potentially leading to reduction of the so-called song complexity, the impacts of noise and urbanization levels on song structural features (such as the number of unique syllable types) may depend on the frequency range of syllables, which require further investigation (Walters et al., 2019).

In addition to altering frequency or structural components of songs, urban birds might also adjust their singing behavior to improve transmission in urban areas (McLaughlin and Kunc, 2013). Birds such as the European robin have been shown to alter their song post sites to higher branches and increase the post site height when exposed to noisy habitats, which may help obtain larger active acoustic space and improve auditory perception under exposure to elevated noise (Mathevon et al., 2005; Polak, 2014). Some bird species are consistently observed singing on the rooftops higher than the neighboring vegetation in urban habitats. Singing at higher posts may improve active space and benefit the auditory of signal receivers (Polak, 2014). Moreover, specialist avian predators are less common in urban habitats, reducing the risks of singing at conspicuous rooftops (Sorace, 2002; Sorace and Gustin, 2009). Thus, frequently utilizing artificial constructions as song post sites could be adaptive behavior in response to urban life.

In this study, we examined the acoustic responses of a common urban songbird, the Oriental Magpie-robin (*Copsychus saularis*; hereafter OMR) to elevated background noise and urbanization levels in the Pearl River Delta region. In the breeding season, OMRs sing complex songs with lower frequencies in the range expected to be impacted by anthropogenic background noise (Bhatt et al., 2000; Bhattacharya et al., 2007; Singh et al., 2019). We explored whether song features are affected by background noise and physical changes to the environment due to urbanization. We selected common song features reported in existing literature to facilitate comparison among studies, including spectral (minimun frequency, maximum frequency and peak frequency) and temporal (song length and syllable rate) characteristics, as well as structural (the number of syllables per song, the number of unique syllable types per song and the number of transitions between syllable types per song, following the song complexity definition of Hill et al. (2018) for the same study species). We predicted that: (1) the minimum frequency of OMR songs would increase with increasing noise levels to avoid signal masking; (2) to reduce reverberations, the maximum frequency of OMR songs should decrease with increasing urbanization levels; and (3) the structural features may be impacted by both the increasing of noise levels and urbanization. Finally, we predicted that choice of song post site might be impacted by noise levels, with individuals in noisier sites more frequenctly singing from song posts on top of artificial constructions which, based on our observations, were generally higher than the tree canopy at our sampling sites. This study provides insights into the behavioral adaptations of birds in a hyper urbanized and rapidly developing region in East Asia, where birds may face extreme conditions in terms of noise and density of urban constructions (Guo et al., 2016; Lee and Park, 2019).

2. Materials and methods

2.1. Study sites

We conducted our fieldwork at 20 sites in seven cities (Shenzhen, Foshan, Guangzhou, Zhongshan, Shaoguan, Qingyuan and Zhuhai) along the Pearl River Delta (111.5°E - 115.5°E, 21.5°N - 25°N) (Fig. 1), one of the most urbanized regions in China, with over 57 million people living within 54,574 km^2 land area. The Pearl River Delta has experienced rapid urbanization with an 81.2% increase of urban built-up area in the last 20 years (Hu et al., 2019).

We classified the level of urbanization of each site using the level of built-up density to evaluate the urbanization level across our study sties (Corbane et al., 2019). Built-up density depicts the urbanization intensity within an area and reflects the physical structure of habitat to some extent. Therefore, built-up density is a key index representing how much the surface of the area has been urbanized (Dutta et al., 2020). Built-up area density was quantified as decimals ranging from 0 to 100 within grids of 250 × 250 m (grid number: 28_5 and 28_6) from open products GHS-BUILT (European Commission Global Human Settlement datasets, GHS BUILT 2015). We extracted built-up density of each sampling site using the point sampling tool in QGIS 3.10 (QGIS.org, 2020).

2.2. Birdsong recording

We recorded songs of OMRs during two breeding seasons (from March to May in 2017 and 2019). At each sampling site, we aimed to record five individuals. We recorded songs opportunistically at each site from dawn to dusk as OMR sing continuously throughout the day. We did not record birds under extreme weather conditions such as typhoons and rainstorms. To avoid recording the same individual more than once, we did not record direct neighbors or any birds within 500 m of another recorded individual. Songs were

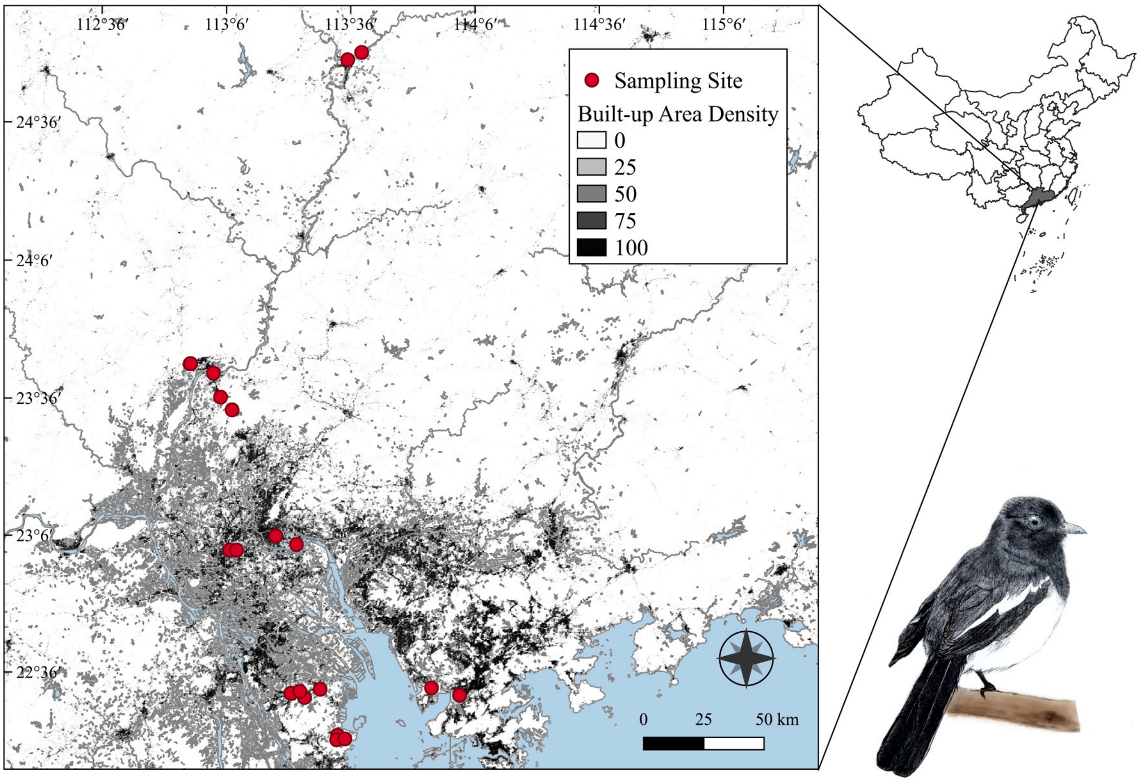

Fig. 1. Sampling map across Pearl River Delta, showing 20 sampling sites (red dots) in seven cities (Shenzhen, Foshan, Guangzhou, Zhongshan, Shaoguan, Qingyuan and Zhuhai) with built-up area density (the grey gradient) at a resolution of 250 m (artwork by Xi Lin). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recorded using a Marantz PMD661 recorder connected with a Sennheiser ME66 short-shotgun microphone or a Telinga Pro 8 MK2 parabolic microphone in 2017, and a SONY PCM-D50 recorder with its internal microphones in 2019. During recording, the microphone was pointed directly at the subject without any apparent obstacles between the bird and the observer. To avoid disturbance by the recorders, we kept a distance of five to ten meters from the target individuals. We recorded each individual bird for at least two minutes or until the focal individual stopped singing or flew away. At the end of each recording, the recordist announced the recording date, time, recording location, as well as the sex of the focal individual and song post site if identified (on the top of a tree or a building). Recordings were saved in WAV format (resolution 24-bit, sample rate 44.1 kHz).

2.3. Noise levels measurements

Immediately following birdsong recording, we measured the background noise levels using a Lutron SL-4013 Sound Level Meter (fast response time, A-weighted, 20 Pa as a reference value) held 1.5 m above the ground. We took the first measurement with the microphone pointing towards the target individual, then rotated through 90 degrees in a clockwise direction to obtain three further measurements. We repeated the same process after one minute. For each recorded individual, we calculated the average noise levels from eight noise measurements. Since the noise levels were measured in the logarithmic unit (dB), all measurements were converted to a linear scale before calculation.

2.4. Acoustic analysis

Song recordings were analyzed using the software Raven Pro 1.5 (Center for Conservation Bioacoustics, 2014). Spectrograms were generated using the following settings: Hann window, window size of 512 samples, and a fast Fourier transformation length of 4096 samples that provided a fine-scale frequency resolution at 10.8 Hz.

We defined OMR songs as long, complex vocal signals, separated from the subsequent vocalization by silent intervals over two seconds (Fig. 2) (Bhattacharya et al., 2007). We measured ten consecutive songs from the song recordings for each individual, skipping any songs that were masked by other signals. For each song recording, we measured three frequency characteristics: minimum frequency, maximum frequency, and peak frequency (i.e., the frequency of the loudest note). Both minimum frequency and maximum frequency were manually determined in spectrogram view, while peak frequency was automatically quantified by Raven software. One challenge of measuring song frequencies in urban areas is that loud, low-frequency background noise may mask the target signal, making it difficult to accurately measure minimum frequency. This would bias the results in the predicted direction, with higher minimum frequencies being measured in noisier areas (induced by lower signal-to-noise ratio, SNR) (Guo et al., 2016). To account for potential measurement errors in noisy sites, we first tested for a correlation between SNR and minimum frequency. We calculated SNR by measuring the in-band power (dB) of songs and that of noise in the interval between songs or in the first second after the song stopped. As we found that SNR significantly correlated with minimum frequency (see Results), we included SNR as an explanatory variable in the models for minimum frequency, maximum frequency and peak frequency to control for this potential measurement errors.

In addition to frequency characteristics, we also quantified two temporal song features including song length, syllable rate (the number of syllables per second) (Sasahara et al., 2012). For structural features, we quantified the number of syllables per song, the number of unique syllable types per song and the number of transitions between syllable types per song (Fig. 3; Hill et al., 2018).

2.5. Statistical analyses

To assess the impacts of noise and urbanization on song structure and behavior, we constructed a set of linear mixed-effect models. In each model, we used each of the song features (i.e., minimum frequency, maximum frequency, peak frequency, song length, syllable rate) as the dependent variable respectively, including average noise levels and urbanization as predictors. As recording quality degradation and elevated noise levels may lead to more measurement errors, we included SNR as an explanatory variable in the models to evaluate the variances explained by song degradation (Guo et al., 2016). We also included individual identity, sampling city, and recording equipment as random effects to control the effects of nested-structured data. The number of syllables per song, the number of

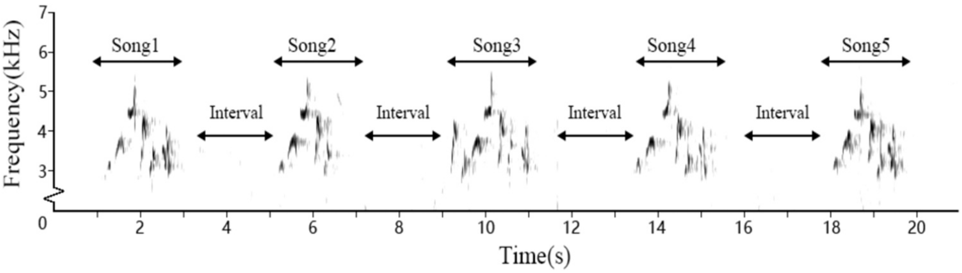

Fig. 2. An example of the consecutive songs of the OMR. Songs (long, complex vocal signals) are separated from each other by silent intervals of ~ 2 s.

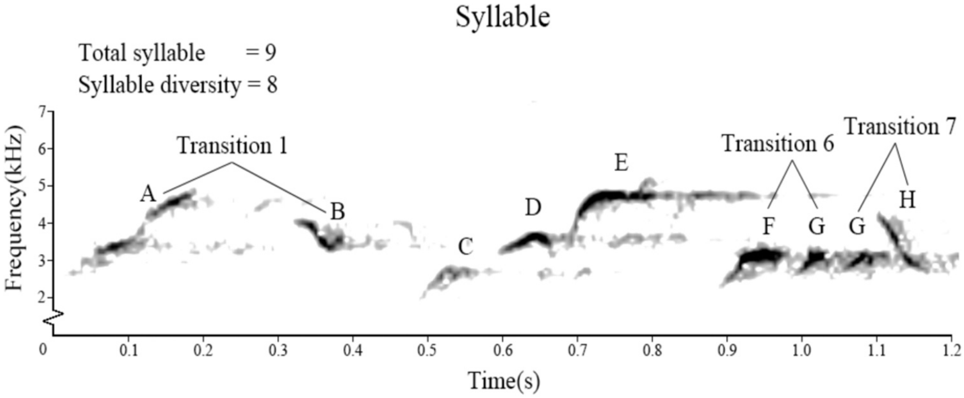

Fig. 3. An OMR song spectrogram showing the method of calculating the number of syllables, syllable diversity, and the number of syllable transitions of each song.

unique syllable types per song and the number of transitions between syllable types per song were count data and violated the linear model assumption that residual errors should normally distributed. Therefore, we separately fitted three generalized linear mixed-effect models for these parameters with logarithm link functions (r package ‘lme4′) (Bates et al., 2015). Predictors and random effects remained the same as described above. All models were fitted using restricted maximum likelihood approach.

To explore whether the choice of song post site was impacted by background noise levels or signal degradation, we only used data from individuals where song post site was identified at the time of recording. We constructed a generalized linear mixed-effect model using the singing post site (on the top of tree or artificial construction) as a binomial dependent variable (tree or building top) and the noise levels as the only independent fixed-effect variables. We included individual identity, sampling city, and recording equipment as random effects to control the effect of nested-structured data. All statistical analyses were conducted in R version 3.6.1 (R Core Team, 2020).

3. Results

Overall, we recorded birdsongs from 87 individuals. We only included recordings with clear spectrograms for further analyses, so in total songs of 82 individuals sampled across the seven cities (average 11.7 individuals/city, Fig. 1) were included. Background noise levels ranged from 38.7 dB to 84.8 dB with an average level of 66.3 dB (across all 82 recording sites).

Across all sites, OMR songs had an average minimum frequency of 2.2 ± 0.4 kHz (mean ± sd), an average maximum frequency of 5.6 ± 0.8 kHz, and an average peak frequency of 3.6 ± 0.5 kHz. An OMR song lasted for 2.3 ± 1.6 s on average and 4.7 ± 1.2 syllables were produced each second. OMR songs had on average 10.5 ± 6.9 syllables per song, 7.6 ± 3.3 syllable types and 8.7 ± 6.6 frequency transitions within a song.

Table 1

Summary of linear mixed-effect models of minimum frequency, maximum frequency, peak frequency, song length and syllable rate, and generalized linear mixed-effect models of syllable count, number of unique syllable types, and syllable transition in testing impacts of background noise levels, urbanization, song post sites and SNR on song features (the significant P value was indicated with *).

Song Features	Variable	Estimate	DF	t (z)	P
Minimum frequency	Noise	0.018	57	3.295	**0.002***
	Urbanization	-0.001	72	-0.311	0.757
	SNR	0.006	809	3.021	**0.003***
Maximum frequency	Noise	0.025	79	2.385	**0.020***
	Urbanization	-0.002	78	-0.474	0.637
	SNR	-0.011	813	-2.849	**0.005***
Peak frequency	Noise	0.008	35	1.745	0.090
	Urbanization	-0.003	36	-1.825	0.076
	SNR	0.003	606	-0.933	0.351
Song length	Noise	-0.004	78	-0.221	0.826
	Urbanization	0.004	64	0.639	0.535
Syllable rate	Noise	-0.007	79	-0.478	0.634
	Urbanization	-0.003	79	-0.604	0.548
Syllable count	Noise	0.002	–	0.258	0.796
	Urbanization	0.000	–	0.063	0.950
N. unique syllable types	Noise	0.003	–	0.646	0.518
	Urbanization	0.001	–	0.760	0.447
Syllable transition	Noise	0.003	–	0.455	0.649
	Urbanization	0.002	–	0.708	0.479

3.1. *Impact of background noise*

There was a significant correlation between SNR and minimum frequency (estimate = 1.663, t = 2.732, $P = 0.006$), so we included SNR as an explanatory factor in our model to control measurement errors. Background noise levels significantly predicted frequency modifications in OMR songs. Minimum frequencies increased with increasing background noise levels (Table 1, Fig. 4A). Maximum frequency also significantly increased with increasing noise levels (Table 1, Fig. 4B). None of the other song features varied background noise levels (Table 1).

3.2. *Impacts of urbanization level*

Built-up density ranged from 0 to 89 across all study sites, confirming that we captured a high variation of urbanization level in our site selection. Despite this variation in urbanization across the sites, none of the song features of OMR varied along the gradient of increasing urbanization (Table 1).

3.3. *Song post site selection*

We identified the song post sites of 63 individuals during recordings. Using this subset data, we found the choice of song post site was not affected by the noise levels (estimate = 0.043, Z = 0.148, P = 0.882).

4. Discussion

We investigated the impacts of background noise levels and urbanization on songs of OMRs. We found that OMRs increased both the minimum and maximum frequency of their songs in response to elevated noise levels, but we did not observe any impact of urbanization level on any song features. Against our predictions, we found no relationship between song post sites and noise levels.

Increasing acoustic signal frequency is one of the most commonly documented responses to elevated urban noise, particularly minimum frequency, and is thought to be an adaptation to avoid signal masking from low-frequency background noise (Guo et al., 2016; Halfwerk and Slabbekoorn, 2009; Lee and Park, 2019; Slabbekoorn and Peet, 2003; Wood and Yezerinac, 2006; but see Brumm and Zollinger, 2013 for a counterargument). Higher minimum frequency is beneficial for masking avoidance in urban habitat by yielding longer communication distance (Nemeth and Brumm, 2009). However, the upwards frequency shift does not guarantee success in urbanized habitats (Moiron et al., 2015; Narango and Rodewald, 2018). Our findings of increasing minimum frequency and maximum frequency of OMR songs suggested OMR may shift its song frequency entirely in response to noise (Dowling et al., 2012).

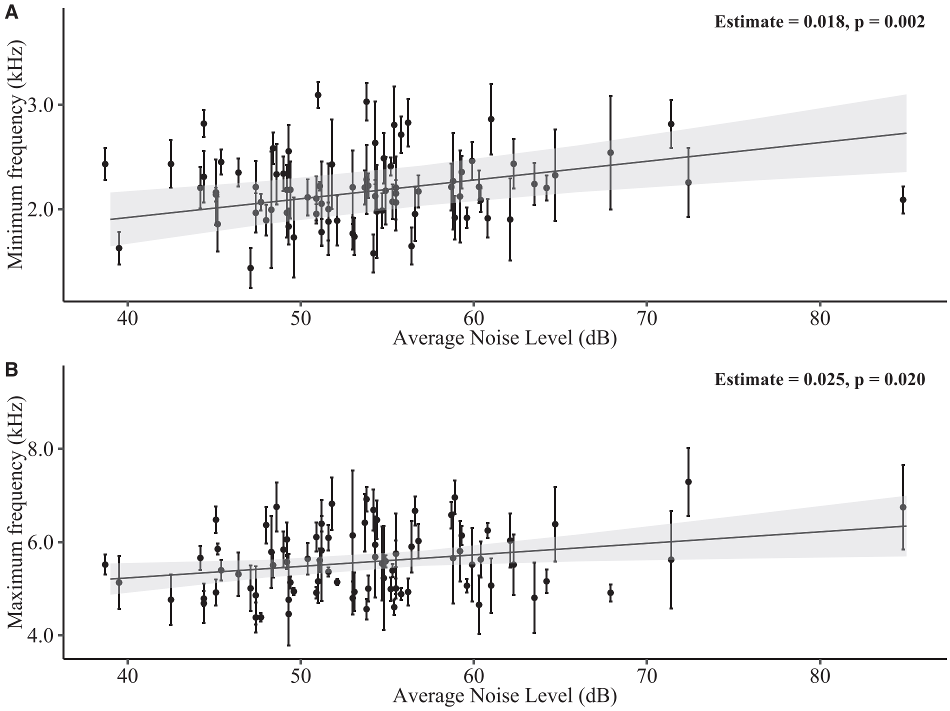

Fig. 4. Both minimum and maximum frequency of OMR song increased with increasing background noise levels along Pearl River Delta (black line: regression line predicted by linear mixed-effect model; grey shade: 95% CI).

The upward shifting OMR songs may fall in the particular sound window with relatively low attenuation, which is overall beneficial for sound transmission (Phillips et al., 2020).

We chose built-up density as our measure of urbanization with the assumption that it accurately depicts the physical structure for signal transmission in urban canyons. However, we did not find that any song features correlated with urbanization levels. It is likely that built-up density does not capture the ground-level details, which may ultimately be more important for shaping bird songs. A similar study investigating the same species simply classified sites as urban or rural, but this is also unlikely to fully describe the variation in physical habitat between sites (Hill et al., 2018). Detailed soundscape information and microclimate factors should be considered in future studies to address urbanization impacts on acoustics signal transmission.

In contrast to the study of Hill et al. (2018) which found that OMR songs were longer, with longer inter-syllable intervals in urban areas, we did not find the song length or syllable rate vary with either noise or urbanization levels. Previous studies have shown mixed results in investigating the relationship between song length (duration) and background noise (Bermúdez-Cuamatzin et al., 2011; Francis et al., 2011; Nemeth and Brumm, 2009; Ríos-Chelén et al., 2013). It is not yet clear the role that song length plays in response to elevated noise level, which likely depends on how such a temporal feature is coded in different species.

Structural features likely play an important role in sexual selection, being considered as an ‘honest signal’ of male quality due to the difficulty of producing complex signals (Catchpole and Slater, 2008). The plasticity that allows species to adapt to novel conditions, such as urban noise, may select for lower song complexity due to the novel stimulus such as elevated noise level (Montague et al., 2013). We therefore predicted that OMRs would sing with less complex songs in noisier areas. Our study population showed larger syllable numbers (10.5 ± 6.9) and more unique syllable types (7.6 ± 3.3) compared to the Uttarakhand population (6.15 ± 2.6, 4.95 ± 1.36, respectively, Singh et al., 2019). However, we found that none of these structural features varied across either a noise or urbanization gradient in our study. There have been few studies that have investigated the impact of noise levels or urbanization on song complexity, but of these studies, species have shown either no impact on structural features or a slight reduction (Kunc and Schmidt, 2020). European robins were found to sing less complex songs in noisy areas (McLaughlin and Kunc, 2013; Montague et al., 2013), while no effect of noise levels on song complexity was found in either zebra finches (*Taeniopygia guttata*) or chiffchaffs (*Phylloscopus collybita*) (Potvin and MacDougall-Shackleton, 2015; Verzijden et al., 2010). A different study on OMRs, based on recordings primarily from cities and nearby rural areas across the native range of the species, similarly found that complexity did not vary between urban (presumably noisy) and rural (presumably quiet) sites (Hill et al., 2018). It is worth noting that song matching (i.e., individuals may modify their singing performance patterns according to different hierarchy levels within the population or singing time) could affect the singing performance and complexity elaboration of OMR (Bhattacharya et al., 2007). In a tonic phrase, individuals may display songs by increasing the volume or length, while in a phasic response they may only sing particular song type. Therefore, identifying song matching among recording sampling is key when discussing the variation of structural features.

Given the potential importance of structural features (i.e. song complexity) for important fitness functions (mate choice and territory defense; Catchpole and Slater, 2008), a reduction in structural features in response to anthropogenic factors could lead to negative fitness consequences (Kunc and Schmidt, 2020). Sexual selection may select for increased complexity in urban dwellers, leading to a trade-off in song optimization (Klingbeil et al., 2020; Moseley et al., 2019). The stage of urbanization may also be important when studying the impacts of urbanization on acoustic communication (Moseley et al., 2019). Future studies with controlled experiments may better control multiple factors and further explore the cause-and-effect relationships between elevated noise levels and song complexity.

Based on our field observation, OMR prefers to sing on the high rooftop to broadcast songs. Yet, we found the choice of song post site was irrelevant to noise level. We neglected the social impacts from the ground predators and conspecific competition. An individual may force to sing higher pitches due to the predation press from prevalent ground predators such as cats (Møller et al., 2010). In addition, singing at high rooftops may indicate the tolerance of high pressure that conspicuously expose to aerial predators (Møller, 2011), which may be preferred by females in urban habitats. It is likely that urban individuals are singing on high rooftops to show off their high tolerance and attract mates.

5. Conclusions

We demonstrated that OMRs adjust their songs in response to urban noise, increasing minimum frequency in noisier areas but not increasing urbanization levels. OMRs show significant frequency shifts in response to background noise. Singing with higher frequency may mitigate the impact of elevated noise levels, but the fitness costs of frequency shifts remain unclear. Temporal and structural features did not vary in response to either noise levels or urbanization. The lack of variation in structural features across different urbanization levels may be due to a trade-off between signal transmission efficiency and important fitness related functions, such as mate selection and territory defense. OMRs did not alter the behavior in selecting song post sites across noise levels. The ability of birds to show plastic responses to noise may be beneficial for signal transmission in noisy urban habitats, but such adjustments could lead to fitness decreases, for example due to reduced reproductive success (Habib et al., 2007; Halfwerk et al., 2011). Future studies using playback experiments could help determine whether plastic or adaptive responses to urban noise cause barriers to conspecific recognition and mate choice, and therefore whether song responses increase or decrease fitness. Nevertheless, this study underscores the necessity of implementing measures to reduce urban noise in rapidly urbanizing regions in China, in order to alleviate its negative effects on birdsongs. Noise control not only matters urban birds’ fitness but is also beneficial to our well-being (Ferraro et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. arXiv Prepr. 1406, 5823. https://doi.org/10.18637/jss.v067.i01.

Bee, M.A., Swanson, E.M., 2007. Auditory masking of anuran advertisement calls by road traffic noise. Anim. Behav. 74, 1765–1776. https://doi.org/10.1016/j.anbehav.2007.03.019.

Benedict, L., Najar, N.A., 2019. Are commonly used metrics of bird song complexity concordant? Ornithology 136, 1–11. https://doi.org/10.1093/auk/uky008.

Bermúdez-Cuamatzin, E., Ríos-Chelén, A.A., Gil, D., Garcia, C.M., 2011. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. Biol. Lett. 7, 36–38. https://doi.org/10.1098/rsbl.2010.0437.

Bhatt, D., Kumar, A., Singh, Y., Payne, R.B., 2000. Territorial songs and calls of the oriental magpie robin Copsychus saularis. Curr. Sci. 78, 722–728.

Bhattacharya, H., Cirillo, J., Subba, B.R., Todt, D., 2007. Song performance rules in the oriental magpie robin (*Copsychus salauris*). Our Nat. 5, 1–13. https://doi.org/10.3126/on.v5i1.791.

Boncoraglio, G., Saino, N., 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Funct. Ecol. 21, 134–142. https://doi.org/10.1111/j.1365-2435.2006.01207.x.

Brumm, H., Zollinger, S.A., 2013. Avian vocal production in noise. Animal Communication and Noise. Springer,, pp. 187–227.

Catchpole, C.K., Slater, P.J.B., 2008. How song develops. Bird Song: Biological Themes and Variations. Cambridge University Cambridge, Cambridge, pp. 49–84. https://doi.org/10.1017/CBO9780511754791.004.

Center for Conservation Bioacoustics, 2014. Raven Pro: Interactive Sound Analysis Software (Version 1.5).

Corbane, C., Pesaresi, M., Kemper, T., Politis, P., Florczyk, A.J., Syrris, V., Melchiorri, M., Sabo, F., Soille, P., 2019. Automated global delineation of human settlements from 40 years of Landsat satellite data archives. Big Earth Data 3, 140–169. https://doi.org/10.1080/20964471.2019.1625528.

Dowling, J.L., Luther, D.A., Marra, P.P., 2012. Comparative effects of urban development and anthropogenic noise on bird songs. Behav. Ecol. 23, 201–209. https://doi.org/10.1093/beheco/arr176.

Dutta, D., Rahman, A., Paul, S.K., Kundu, A., 2020. Estimating urban growth in peri-urban areas and its interrelationships with built-up density using earth observation datasets. Ann. Reg. Sci. 65, 67–82. https://doi.org/10.1007/s00168-020-00974-8.

Fernández-Juricic, E., Poston, R., De Collibus, K., Morgan, T., Bastain, B., Martin, C., Jones, K., Treminio, R., 2005. Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western US. Urban Habitats 3, 1541–7115.

Ferraro, D.M., Miller, Z.D., Ferguson, L.A., Taff, B.D., Barber, J.R., Newman, P., Francis, C.D., 2020. The phantom chorus: Birdsong boosts human well-being in protected areas: phantom chorus improves human well-being. Proc. R. Soc. B Biol. Sci. 287. https://doi.org/10.1098/rspb.2020.1811.

Francis, C.D., Ortega, C.P., Cruz, A., 2011. Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biol. Lett. 7, 850–852. https://doi.org/10.1098/rsbl.2011.0359.

Gil, D., Brumm, H., 2014. Acoustic communication in the urban environment: patterns, mechanisms, and potential consequences of avian song adjustments. Avian Urban Ecology. Oxford University Press, Oxford, pp. 69–83.

Grabarczyk, E.E., Gill, S.A., 2019. Anthropogenic noise affects male house wren response to but not detection of territorial intruders. PLoS One 14, 1–17. https://doi.org/10.1371/journal.pone.0220576.

Gross, K., Pasinelli, G., Kunc, H.P., 2010. Behavioral plasticity allows short-term adjustment to a novel environment. Am. Nat. 176, 456–464. https://doi.org/10.1086/655428.

Guo, F., Bonebrake, T.C., Dingle, C., 2016. Low frequency dove coos vary across noise gradients in an urbanized environment. Behav. Process. 129, 86–93.

Habib, L., Bayne, E.M., Boutin, S., 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla. J. Appl. Ecol. 44, 176–184. https://doi.org/10.1111/j.1365-2664.2006.01234.x.

Halfwerk, W., Slabbekoorn, H., 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. Anim. Behav. 78, 1301–1307. https://doi.org/10.1016/j.anbehav.2009.09.015.

Halfwerk, W., Slabbekoorn, H., 2013. The impact of anthropogenic noise on avian communication and fitness. Avian Urban Ecol. 84–97. https://doi.org/10.1093/acprof:osobl/9780199661572.003.0007.

Halfwerk, W., Holleman, L.J.M., Lessells, Ck.M., Slabbekoorn, H., 2011. Negative impact of traffic noise on avian reproductive success. J. Appl. Ecol. 48, 210–219. https://doi.org/10.1111/j.1365-2664.2010.01914.x.

Hamao, S., Watanabe, M., Mori, Y., 2011. Urban noise and male density affect songs in the great tit Parus major. Ethol. Ecol. Evol. 23, 111–119. https://doi.org/10.1080/03949370.2011.554881.

Hill, S.D., Aryal, A., Pawley, M.D.M., Weihong, J.I., 2018. So much for the city: urban–rural song variation in a widespread Asiatic songbird. Integr. Zool. 13, 194–205. https://doi.org/10.1111/1749-4877.12284.

Hu, M., Li, Z., Wang, Y., Jiao, M., Li, M., Xia, B., 2019. Spatio-temporal changes in ecosystem service value in response to land-use/cover changes in the Pearl River Delta. Resour. Conserv. Recycl. 149, 106–114.

Hu, Y., Cardoso, G.C., 2010. Which birds adjust the frequency of vocalizations in urban noise? Anim. Behav. 79, 863–867.

Kleist, N.J., Guralnick, R.P., Cruz, A., Francis, C.D., 2016. Anthropogenic noise weakens territorial response to intruder's songs. Ecosphere 7. https://doi.org/10.1002/ecs2.1259.

Klingbeil, B.T., La Sorte, F.A., Lepczyk, C.A., Fink, D., Flather, C.H., 2020. Geographical associations with anthropogenic noise pollution for North American breeding birds. Glob. Ecol. Biogeogr. 29, 148–158. https://doi.org/10.1111/geb.13016.

Kunc, H.P., Schmidt, R., 2020. Species sensitivities to a global pollutant: A meta-analysis on acoustic signals in response to anthropogenic noise. Glob. Change Biol. 27, 675–688. https://doi.org/10.1111/gcb.15428.

Lee, C., Park, C.R., 2019. An increase in song pitch of eastern great tits (*Parus minor*) in response to urban noise at Seoul, Korea. Urban Ecosyst. 22, 227–233. https://doi.org/10.1007/s11252-018-0809-z.

Lohr, B., Wright, T.F., Dooling, R.J., 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Anim. Behav. 65, 763–777. https://doi.org/10.1006/anbe.2003.2093.

Luther, D.A., Phillips, J., Derryberry, E.P., 2016. Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. Behav. Ecol. 27, 332–340. https://doi.org/10.1093/beheco/arv162.

Mathevon, N., Dabelsteen, T., Blumenrath, S.H., 2005. Are high perches in the blackcap Sylvia atricapilla song or listening posts? A sound transmission study. J. Acoust. Soc. Am. 117, 442–449. https://doi.org/10.1121/1.1828805.

McLaughlin, K.E., Kunc, H.P., 2013. Experimentally increased noise levels change spatial and singing behaviour. Biol. Lett. 9, 20120771 https://doi.org/10.1098/rsbl.2012.0771.

Moiron, M., González-Lagos, C., Slabbekoorn, H., Sol, D., 2015. Singing in the city: high song frequencies are no guarantee for urban success in birds. Behav. Ecol. 26, 843–850. https://doi.org/10.1093/beheco/arv026.

Møller, A.P., 2011. Song post height in relation to predator diversity and urbanization. Ethology 117 (6), 529–538.

Møller, A.P., Erritzøe, J., Nielsen, J.T., 2010. Causes of interspecific variation in susceptibility to cat predation on birds. Chine Birds 1 (2), 97–111.

Montague, M.J., Danek-Gontard, M., Kunc, H.P., 2013. Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. Behav. Ecol. 24, 342–348. https://doi.org/10.1093/beheco/ars169.

Morton, E.S., 1975. Ecological sources of selection on avian sounds. Am. Nat. 109, 17–34. https://doi.org/10.1086/282971.

Moseley, D.L., Phillips, J.N., Derryberry, E.P., Luther, D.A., 2019. Evidence for differing trajectories of songs in urban and rural populations. Behav. Ecol. 30, 1734–1742. https://doi.org/10.1093/beheco/arz142.

Narango, D.L., Rodewald, A.D., 2018. Signal information of bird song changes in human-dominated landscapes. Urban Ecosyst. 21, 41–50. https://doi.org/10.1007/s11252-017-0698-6.

Nemeth, E., Brumm, H., 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Anim. Behav. 78, 637–641. https://doi.org/10.1016/j.anbehav.2009.06.016.

Nemeth, E., Pieretti, N., Zollinger, S.A., Geberzahn, N., Partecke, J., Mirand, A.C., Brumm, H., 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proc. R. Soc. B Biol. Sci. 280, 1–7. https://doi.org/10.1098/rspb.2012.2798.

Nolan, P.M., Hill, G.E., 2004. Female choice for song characteristics in the house finch. Anim. Behav. 67, 403–410. https://doi.org/10.1016/j.anbehav.2003.03.018.

Parris, K.M., McCarthy, M.A., 2013. Predicting the effect of urban noise on the active space of avian vocal signals. Am. Nat. 182, 452–464.

Phillips, J.N., Rochefort, C., Lipshutz, S., Derryberry, G.E., Luther, D., Derryberry, E.P., 2020. Increased attenuation and reverberation are associated with lower maximum frequencies and narrow bandwidth of bird songs in cities. J. Ornithol. 161, 593–608. https://doi.org/10.1007/s10336-020-01751-2.

Polak, M., 2014. Relationship between traffic noise levels and song perch height in a common passerine bird. Transp. Res. Part D. Transp. Environ. 30, 72–75. https://doi.org/10.1016/j.trd.2014.05.004.

Potvin, D.A., MacDougall-Shackleton, S.A., 2015. Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches. J. Exp. Zool. Part A Ecol. Genet. Physiol. 323, 722–730. https://doi.org/10.1002/jez.1965.

Potvin, D.A., Parris, K.M., Mulder, R.A., 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*). Proc. R. Soc. B Biol. Sci. 278, 2464–2469. https://doi.org/10.1098/rspb.2010.2296.

QGIS.org, 2020. QGIS Geographic Information System. QGIS Assoc.

R Core Team, 2020. R: A language and environment for statistical computing.

Richards, D.G., Wiley, R.H., 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. Am. Nat. 115, 381–399.

Ríos-Chelén, A.A., Quirós-Guerrero, E., Gil, D., Macías Garcia, C., 2013. Dealing with urban noise: Vermilion flycatchers sing longer songs in noisier territories. Behav. Ecol. Sociobiol. 67, 145–152. https://doi.org/10.1007/s00265-012-1434-0.

Ríos-Chelén, A.A., Lee, G.C., Patricelli, G.L., 2015. Anthropogenic noise is associated with changes in acoustic but not visual signals in red-winged blackbirds. Behav. Ecol. Sociobiol. 69, 1139–1151. https://doi.org/10.1007/s00265-015-1928-7.

Sasahara, K., Cody, M.L., Cohen, D., Taylor, C.E., 2012. Structural design principles of complex bird songs: a network-based approach. PLoS One 7, 44436. https://doi.org/10.1371/journal.pone.0044436.

Schlichting, C.D., 1989. Phenotypic integration. Bioscience 39, 460–464.

Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc. Natl. Acad. Sci. U.S.A. 109, 16083–16088. https://doi.org/10.1073/pnas.1211658109.

Singh, A., Bhatt, D., Sethi, V.K., 2019. Singing behaviour of the oriental magpie robin (*Copsychus saularis*). J. Ornithol. 160, 185–193. https://doi.org/10.1007/s10336-018-1595-3.

Slabbekoorn, H., Peet, M., 2003. Ecology: birds sing at a higher pitch in urban noise. Nature 424, 267, 267–267.

Slabbekoorn, H., Ripmeester, E.A.P., 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Mol. Ecol. 17, 72–83. https://doi.org/10.1111/j.1365-294X.2007.03487.x.

Slabbekoorn, H., Yeh, P., Hunt, K., 2007. Sound transmission and song divergence: a comparison of urban and forest acoustics. Condor 109, 67–78. https://doi.org/10.1093/condor/109.1.67.

Soma, M., Garamszegi, L.Z., 2011. Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. Behav. Ecol. 22, 363–371. https://doi.org/10.1093/beheco/arq219.

Sorace, A., 2002. High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fenn. 79, 60–71.

Sorace, A., Gustin, M., 2009. Distribution of generalist and specialist predators along urban gradients. Landsc. Urban Plan. 90, 111–118. https://doi.org/10.1016/j.landurbplan.2008.10.019.

Verzijden, M.N., Ripmeester, E.A.P., Ohms, V.R., Snelderwaard, P., Slabbekoorn, H., 2010. Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. J. Exp. Biol. 213, 2575–2581. https://doi.org/10.1242/jeb.038299.

Walters, M.J., Guralnick, R.P., Kleist, N.J., Robinson, S.K., 2019. Urban background noise affects breeding song frequency and syllable-Type composition in the Northern Mockingbird. Condor 121, duz002. https://doi.org/10.1093/condor/duz002.

Warren, P.S., Katti, M., Ermann, M., Brazel, A., 2006. Urban bioacoustics: It's not just noise. Anim. Behav. 71, 491–502. https://doi.org/10.1016/j.anbehav.2005.07.014.

Wiley, R.H., Richards, D.G., 1982. Acoustic Communication in Birds, Production, Perception, and Design Features of Sounds. Academic Press, New York, NY.

Wood, W.E., Yezerinac, S.M., 2006. Song sparrow (*Melospiza melodia*) Song varies with urban noise. Auk 123, 650–659. https://doi.org/10.1093/auk/123.3.650.

Yip, D.A., Bayne, E.M., Sólymos, P., Campbell, J., Proppe, D., 2017. Sound attenuation in forest and roadside environments: Implications for avian point-count surveys. Condor 119, 73–84. https://doi.org/10.1650/CONDOR-16-93.1.

Yu, X., Shen, M., Shen, W., Zhang, X., 2020. Effects of land urbanization on smog pollution in China: estimation of spatial autoregressive panel data models. Land 9, 337.

Zwart, M.C., Dunn, J.C., McGowan, P.J.K., Whittingham, M.J., 2016. Wind farm noise suppresses territorial defense behavior in a songbird. Behav. Ecol. 27, 101–108. https://doi.org/10.1093/beheco/arv128.