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Higher-pitched bird song towards the coast supports a role for selection in ocean noise avoidance

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ABSTRACT

Effective communication in birds is often hampered by background noise, with much research focusing on the effect of anthropogenic noise on passerine bird song. Continuous low-pitch natural noise can drive changes in both spectral and temporal patterning of bird vocalisations, but the extent to which these effects may also affect birds that lack vocal learning is not well understood. We used a gradient of exposure to natural low-frequency noise to assess whether it exerts selective pressure on innate vocalisations. We tested whether three species of *Pogoniulus* tinkerbirds adapt their song when exposed to continuous low-frequency noise from ocean surf. We show that dominant frequency increases the closer birds are to the coast in at least two species, indicating that ocean surf sound may apply a selective pressure on songs. Tinkerbirds adapt their songs by increasing dominant frequency to avoid masking by ambient noise, therefore improving long-range communication. Our study provides evidence that natural ambient noise affects vocalisations in birds whose songs develop innately. We believe that our results can also be extrapolated in the context of anthropogenic noise pollution, hence providing a baseline for the study of the effects of low-frequency ambient noise on birds that lack vocal learning.

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Geophony; acoustic adaptation; tinkerbirds; non-passerine; acoustic communication; background noise

Introduction

Many species rely on acoustic communication to accomplish functions that are crucial for their survival (Bradbury and Vehrencamp 2011). Bird song, for instance, has been shown to mediate behaviours involved in mate attraction, competition for partners, food and space (Catchpole and Slater 1995; Naguib and Riebel 2014); even though it may also function to coordinate group movements and to warn other individuals against potential threats (Naguib and Wiley 2001; Bradbury and Vehrencamp 2011; Halfwerk et al. 2018). An effective signal transfer is therefore essential to ensure the prompt behavioural response of the receiver.

The transfer of clear signals might be hampered by the sound transmission properties of the environment, which may degrade signals (Brumm and Naguib 2009), or by

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Supplemental data for this article can be accessed here.

interference from environmental noise (Brumm and Slabbekoorn 2005; Blumstein et al. 2011). Under the latter scenario, sounds similar in frequency and amplitude can have a masking effect and potentially lead to the transmission of incomplete or incorrect information (Slabbekoorn 2013). Such effects have a strong effect on vocal behaviour of birds (Patricelli and Blickley 2006; Slabbekoorn 2013). Indeed, experiments have shown birds in one environment with a specific ambient noise profile respond less to songs adapted to different ambient noise profiles than to those adapted to similar ambient noise profiles (Kirschel et al. 2011). Therefore, loud and continuous background noise impose strong selective pressures on bird song to increase its effectiveness in noisy environments (Slabbekoorn and Smith 2002a; Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Slabbekoorn and den Boer-visser 2006; Slabbekoorn and Ripmeester 2008; Halfwerk and Slabbekoorn 2009; Nemeth and Brumm 2010).

Birds react to low-frequency ambient noise pressure in different ways (Brumm and Slabbekoorn 2005; Swaddle et al. 2015). Some have been shown to increase their minimum frequency (Slabbekoorn and den Boer-visser 2006; Nemeth and Brumm 2009, 2010; Hu and Cardoso 2010; Mendes et al. 2011; Ríos-Chelén et al. 2012), maximum frequency (Francis et al. 2011; Mendes et al. 2011) and others their dominant frequency (Nemeth and Brumm 2009; Hu and Cardoso 2010; Proppe et al. 2011, 2012; LaZerte et al. 2016, 2017; Luther et al. 2016; de Tolentino et al. 2018) in response to background noise. Increases in frequency may, however, be a side effect of singing at higher amplitude in noisy environments (Nemeth and Brumm 2010) – the Lombard Effect (Brumm and Zollinger 2011; Zollinger and Brumm 2011) – as amplitude and song frequency are often correlated (Beckers et al. 2003; Amador et al. 2008; Zollinger et al. 2012). Other adaptations to low-frequency ambient noise include increasing signal redundancy (Brumm and Slater 2006; Deoniziak and Osiejuk 2016), singing more often (Deoniziak and Osiejuk 2019), for longer periods (Brumm and Slater 2006; Nemeth and Brumm 2009; Sierro et al. 2017) or at specific time intervals (Dominoni et al. 2016).

Changes in vocal parameters can result from different mechanisms, for instance, response to background noise might be plastic, as found in House Finches (*Carpodacus mexicanus*) (Bermúdez-Cuamatzin et al. 2009), or learned, as demonstrated in Black-capped chickadees (*Poecile atricapillus*) (LaZerte et al. 2016) and White-crowned sparrows (*Zonotrichia laucophyrs*) (Moseley et al. 2018). Shifts in signal design might also arise because selection may favour individuals that minimise the masking effect of ambient noise (Slabbekoorn and Smith 2002a; Kirschel, Blumstein, Cohen, et al. 2009; Kirschel et al. 2011). This scenario is compatible with the song developing by sensory drive (Endler 1992), a mechanism which appears to have shaped acoustic signals of many Neotropical suboscines (Seddon 2005) that lack song learning capabilities (Touchton et al. 2014).

Most studies on the effects of noise on acoustic communication have addressed this issue by looking at the effects of anthropogenic noise pollution. However, natural sources of noise may have similar masking effects on animal signalling (Davidson et al. 2017; Goutte et al. 2018). For instance, Halfwerk et al. (2016) show multimodal communication between male Tungara frogs (*Physalaemus pustulosus*) was hindered when geophonic noise from windy and rainy conditions was simulated. Other studies on birds and other taxa have also shown an effect of natural background noise on communication (Lengagne et al. 1999; Lengagne and Slater 2002; Brumm and Slater 2006; Feng et al. 2006; Kirschel, Blumstein, Cohen, et al. 2009; Davidson et al. 2017). Therefore, natural ambient noise is likely to be as impactful as anthropogenic noise and with such noise present over evolutionary timescales it is likely to have evolutionary implications for acoustic communication (Davidson et al. 2017).

To date, the study of the effects of ambient noise on bird signalling has focused mostly on oscine passerines that learn their songs by way of auditory feedback (Hu and Cardoso 2010; Ríos-Chelén et al. 2012). By contrast, there is scant information on how taxa that lack vocal learning, such as suboscines and many non-passerines birds, cope with high background noise levels (Gentry et al. 2018; de Tolentino et al. 2018). Studies on non-passerines include those on King penguins (*Aptenodytes*) (Lengagne et al. 1999) and Tawny owls (Lengagne and Slater 2002). In both cases, responses to increased ambient noise were in temporal patterning of their vocalisations. King penguins increased both the number of calls and syllables per call emitted under strong winds, whereas Tawny owls reduced call rates under rainy conditions because the interference of rain noise increased the unreliability of the information conveyed in their calls. Hu and Cardoso (2010) did document changes in the frequency domain in response to anthropogenic noise in a non-passerine by observing an increase in minimum frequency in urban rainbow lorikeets (*Tricoglossus haematodus*) and eastern rosellas (*Platycercus eximius*), two Psittaculidae (Order: Psittaciformes). However, parrots, like hummingbirds and oscine passerines, are capable of vocal learning (Nottebohm 1972; Kroodsma 1982; Catchpole and Slater 1995; Saranathan et al. 2007) and therefore may respond plastically to increased background noise levels (Osmanski and Dooling 2009; Scarl and Bradbury 2009). One study attributed differences in frequency in a non-passerine bird with innate vocalisations on the effects of environmental noise. Willets (*Tringa semipalmata*) of the subspecies breeding on the Atlantic coast sing at higher frequencies and trill rate than those breeding inland (Western et al. 1998; Douglas and Conner 1999; Lowther et al. 2001). The authors attributed the differences to adaptive changes that might facilitate communication among individuals in the presence of constant surf sound. Although these might represent plausible explanations, with the populations geographically isolated, other evolutionary forces, including genetic drift, might contribute to shape Willet vocalisations. Although birds not capable of learning such as suboscines and many non-passerines may be more vulnerable to the effects of increased background noise given their lower ability to adapt their signals (Ríos-Chelén et al. 2012), little is known about the mechanisms that ensure efficient communication under noisy conditions in such taxa.

Here, we investigate whether *Pogoniulus* tinkerbirds (Family: Lybiidae; Order: Piciformes) might adapt the frequency of their songs in response to increased geophonic ambient noise from ocean surf. The low-frequency acoustical energy generated by ocean waves can travel for several kilometres and can even lead to an increase in temperature in the higher atmosphere (Daniels 1952). Background noise from ocean surf has already been shown to affect communication in other systems (Gossard and Hooke 1975; Brumm 2013). For instance, Douglas and Conner (1999) found that eastern Willets have a shorter song than western willet, an adaptation that would facilitate the Willet's communication, because more song replicates can be fitted into the sound interval between surf-generated noise, whereas white-crowned sparrows have been shown to increase song performance at coastal sites in response to increased ambient noise (Davidson et al. 2017). Tinkerbirds emit a simple, single pitch, stereotyped song that develops innately (Kirschel, Blumstein, and Smith 2009; Kirschel, Nwankwo, et al. 2020; Nwankwo et al. 2019). Because of the absence of auditory feedback in song development, adaptation to noisy environments is unlikely to involve a learned or plastic response in frequency (Nottebohm 1972). Instead, any variation in tinkerbird song that would minimise the masking effect of noise may reflect an adaptive change. Hence, our study specifically addresses whether there could be a selective pressure on tinkerbird song of low-frequency surf sound by focusing on species whose songs are innately developed. Previous work has found evidence for character displacement in tinkerbird song frequency when two species coexist at high densities, consistent with a role of competitive or reproductive interference of songs of similar frequencies (Kirschel, Blumstein, and Smith 2009; Kirschel, Nwankwo, et al. 2020). First, we test whether yellow-throated tinkerbird (*Pogoniulus subsulphureus*) adjusts its song along a gradient of exposure to low-frequency ambient noise emanating from ocean surf in Atlantic coast populations. We also measure local ambient noise to test for a gradient in noise levels with distance and whether there is a direct relationship of low-frequency surf sound and song frequency. We then test whether there is a relationship between song frequency and distance from the coast in *P. subsulphureus*, as well as in two further species recorded close to the Indian Ocean coast, the red-fronted (*P. pusillus*) and the coastal subspecies of yellow-rumped tinkerbird (*P. bilineatus fischeri*).

Materials and methods

Study species

Pogoniulus tinkerbirds are small African barbets (Family: Lybiidae) that are widely distributed throughout Sub-Saharan Africa. They are sedentary (Short and Horne 2002), and prefer to feed on mistletoe, though they also take small invertebrates (Godschalk 1985; Dowsett-Lemaire 1988; Short and Horne 2001). *P. subsulphureus* (~10 g) (hereafter *subsulphureus*) strictly inhabits tropical lowland rainforests in Central and Western Africa (Short and Horne 2002; Kirschel, Nwankwo, et al. 2020), whereas *P. pusillus* (~10 g) (hereafter *pusillus*) occupies savanna woodland and secondary forest below 2000 metres. On the other hand, *P. b. fischeri* (~12 g) (hereafter *fischeri*) only occurs in coastal forests in southern Kenya and on the island of Zanzibar (Nwankwo et al. 2018).

Song collection and acoustical analysis

We obtained recordings of *P. subsulphureus, P. pusillus* and *P. b. fischeri* from a total of 15 coastal locations in Cameroon, Kenya and Tanzania (Figure 1), in tropical moist forest. The habitat is characterised in both countries by dense vegetation, which is expected to favour lower frequency song (e.g. Kirschel, Blumstein, Cohen, et al. 2009, because higher frequencies attenuate more than low frequencies in dense vegetation (Slabbekoorn and Smith 2002b; Bradbury and Vehrencamp 2011), and it is not expected to influence song any differently between the two regions. We also obtained fifty ambient noise recordings (spanning from ~ 718 m to 6,300 m from the shore) from four locations in Cameroon by taking 1-minute long recordings every hour from

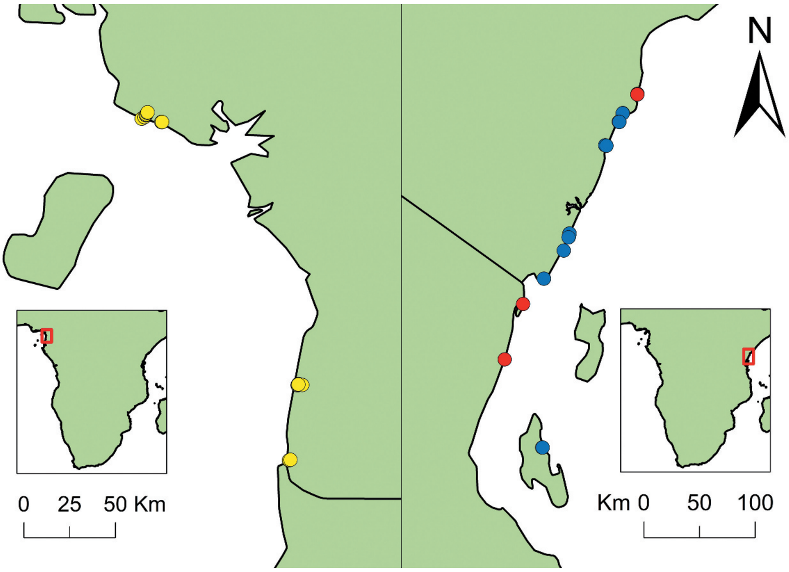

Figure 1. Map of recording localities in Cameroon (left) and Kenya and Tanzania (right). Coloured points represent recording locations of *P. subsulphureus* (yellow), *P. pusillus* (red), and *P. b. fischeri* (blue).

7:00 to 12:00, holding the microphone horizontally every 10 seconds in each of the four cardinal direction (North, South, East, West) and then vertically upwards, as described in Kirschel, Blumstain, Cohen, et al. (2009). Ambient noise and *subsulphureus* songs were recorded using a Marantz PMD670 a Sennheiser ME67, while *pusillus* and *fischeri* songs were recorded with a Marantz PMD661 recorder with a MKH8050 or MKH8020 microphone, the latter housed in a Telinga parabolic reflector. The recordings of these two species had originally been obtained for use in parallel studies (Nwankwo et al. 2018, Kirschel et al. unpublished data), without accompanying ambient noise recordings, but the proximity of some of the recordings to the coast allowed for the opportunity to test for its effect on their song frequency.

Recordings were made within 30 m from the singing tinkerbird, saved as WAV files and imported into Raven Pro 1.6 (Center for Conservation Bioacoustics 2019), in which songs were measured using its built-in automated energy detectors. We caution, however that we also included 10 recordings saved as MP3 files, and measurements of such recordings might be affected by sound compression (Araya-Salas et al. 2019). Target signal parameters were set as follows: minimum and maximum frequencies spanned from 800 to 1700 Hz according to the species, minimum duration was 0.03 s and maximum duration 0.3; minimum separation was set to 0.01 s for *fischeri*, 0.05 s for *subsulphureus* and 0.25 for *pusillus*. The signal-to-noise ratio (SNR) threshold was set in order to detect the maximum number of notes and varied depending on the background noise levels on the recording. Most of the detections were obtained setting the SNR above the threshold of 10–20 dB. Detections were visually inspected and modified to match the actual begin and end times using the waveform as a reference when automatic detections did not coincide with actual begin and end times. We chose this instead of a manualmeasurement approach since the latter can lead to biased measurements (Brumm et al. 2017; Ríos-Chelén et al. 2017). Raven provided peak frequency measurements from the spectrogram view (DFT size: 4096; Window: Hanning, 3 dB; overlap: 50) and we obtained the dominant frequency by calculating the mean from peak frequency values of all notes detected on each recording.

From the 50 ambient noise recordings, six were removed because of loud anthropogenic traffic noise in the background and another was excluded because of loud stream waterfall noise, both of which obscured natural surf sound. From the remaining recordings, we selected and merged together five high-quality 5 s intervals per direction. In one instance we included just the four 5 s intervals from cardinal directions, because the vertical recording was beset by mechanical interference. Each 25 s ambient noise recording cut was then imported into R and the ambient noise amplitude (dBA) at 1 kHz was calculated using the noise profile function provided in the baRulho R package (Araya-Salas 2020). Subsequently, we used amplitude at 1 kHz (a measure of low-frequency noise) as covariate in statistical models.

Spatial distance calculation

GPS coordinates of singing tinkerbirds and ambient noise recorded in the field were obtained using a Garmin GPSMap. We imported the coordinates into Google Earth Pro and calculated the closest distance from each recording location to the coastline using its built-in measuring tool (see Table S1 for distance from the shore of each recording).

Statistical analysis

To test whether ocean surf sound affects tinkerbird song, we first assessed whether dominant frequency of *subsulphureus*' coastal population of in Cameroon increased with background noise amplitude measured at 1 kHz and whether the ambient noise (1 kHz) from Cameroon sites, for which ambient noise recordings were available, decreased with increased distance from the coast . We then measured the effect of distance from the coast on dominant frequency of *subsulphureus, pusillus* and *fischeri* songs. This effect was measured within approximately 6 km from the coast as ambient noise recordings were collected within that range and songs of birds further from the coast are likely to be influenced more by other factors, including vegetation density and elevation (Kirschel, Blumstein, Cohen, et al. 2009) and interactions with congenerics (Kirschel, Blumstein and Smith 2009), than by distant surf sound. We assumed that, if ocean surf sound has an effect on their song, dominant frequency would decrease as the distance from the coast increases.

Using Gaussian generalised linear mixed models (GLMM) in the glmmTMB R package (Brooks et al. 2017), we first measured the effect of ambient noise (at 1 kHz) on dominant frequency of *subsulphureus* (log-transformed) from Cameroon, setting the former as fixed factor and the latter as the response variable. Here, we set Bird ID nested in location as random factors to account for individual variation as well as variation among field sites. We also fitted a Gaussian GLMM to test for the effect of distance from the coast (log-transformed) on ambient noise amplitude at 1 kHz in Cameroon coastal sites using the latter as response variable and location as a random effect. We then assessed the relationships

Table 1. Gaussian generalised linear mixed models output showing the relationship between (**a**) *subsulphureus* dominant frequency and ambient noise measured at 1 kHz; (**b**) surf sound ambient noise and (log) distance from the coast in Cameroon and (**c**) dominant frequency of the three species, (log) distance from the coast and their interaction. Significant *p*-values are represented in bold.

	Estimate	St. error	z	p
a) Response:				
P. subsulphureus				
(log) dominant frequency				
N = 39				
Intercept	3.247	0.034	94.76	**<0.001**
Ambient amplitude 1 kHz	0.001	0.0004	2.93	**0.003**
b) Response:				
Ambient amplitude 1 kHz				
N = 34				
Intercept	−69.56	1.58	−43.93	**<0.001**
(log) distance	−3.34	0.59	−5.67	**<0.001**
c) Response:				
(log) dominant frequency				
N = 94				
Intercept	3.142	0.003	926.6	**<0.001**
Species: *P. pusillus*	−0.024	0.007	−3.4	**<0.001**
Species: *P. b. fischeri*	−0.105	0.005	−17.7	**<0.001**
(log) distance	−0.008	0.001	−4.5	**<0.001**
P. pusillus * (log) distance	−0.002	0.005	−0.4	0.662
P. b. fischeri * (log) distance	0.005	0.004	1.3	0.196

between dominant frequency for all three species and distance from the coast fitting Gaussian GLMM using (log) dominant frequency as dependent variable and (log) distance from the coast, species (categorical with three levels: 1) *subsulphureus*, 2) *pusillus* and 3) *fischeri*) and their interaction, as fixed factors. Also here, we set Bird ID nested in location as random factors. All models were selected according to the lowest corrected Akaike Information Criterion score. Model assumptions were validated using the functions provided in DHARMa (Harting 2019), and back transformed model estimates (Table S2) and graphical representations of fitted coefficients were produced with the Effects package (Fox and Weisberg 2018) in R.

Results

We obtained 94 recordings (45 *subsulphureus*, 20 *pusillus* and 29 *fischeri*) from a total of 68 individuals (36 *subsulphureus*, 15 *pusillus* and 17 *fischeri*) at coastal sites in Cameroon and Kenya (Figure 1). We found a significant positive relationship between *subsulphureus* dominant frequency and ambient noise amplitude at 1 kHz (Table 1a, Figure 2a) as well as a highly significant decrease in low-frequency ambient noise (1 kHz) with log-distance from the coast in Cameroon (Table 1b, Figure 2b)

We also found a significant negative effect of distance from the coast on dominant frequency, with tinkerbirds singing at higher frequencies closer to the coast (Figure 3, Table 1c, see Table S3 for model selection table). In addition, *pusillus* and *fischeri* sang at lower frequencies compared to *subsulphureus*, but there was no significant difference in the effect of distance from the coast on *pusillus* and *fischeri* song compared to *subsulphureus* song.

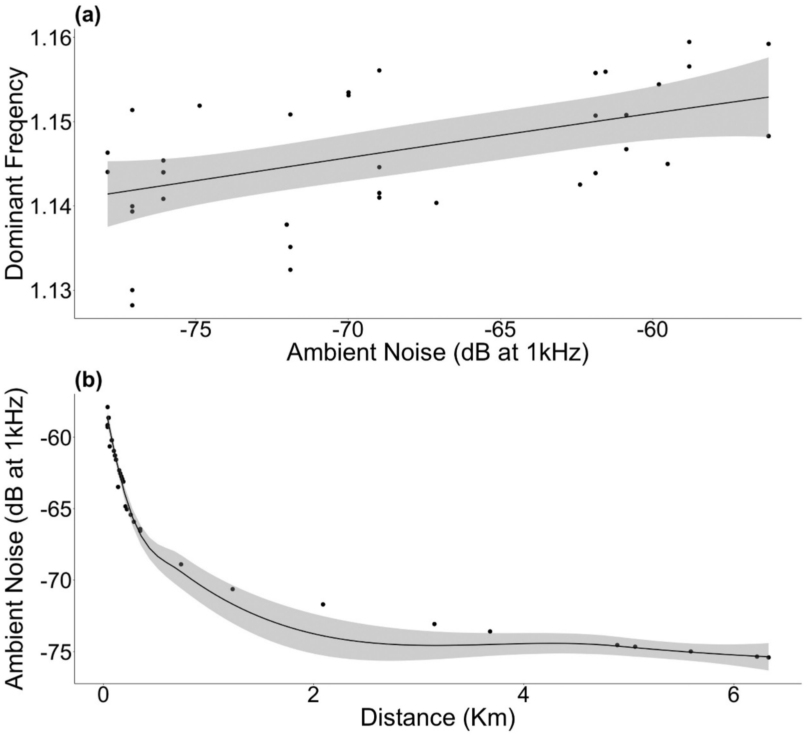

Figure 2. Plot illustrating fitted coefficients and 95% confidence intervals from the Gaussian GLMM testing **a)** the relationship between *subsulphureus* dominant frequency (log kHz) and ambient noise and **b)** the relationship between ambient noise and distance from the coast in Cameroon.

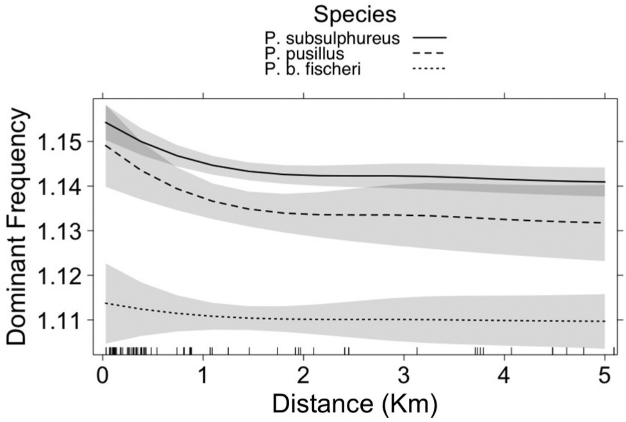

Figure 3. Plot illustrating fitted coefficients and 95% confidence interval from the Gaussian GLMM assessing the relationship between dominant frequency (log kHz) and distance from the coast in *subsulphureus, pusillus* and *fischeri* before controlling for other possible effects.

Discussion

We have shown an overall effect of distance from the coast on dominant frequency, with tinkerbirds singing at higher frequencies the closer they are to the coast and as the amplitude of low-frequency ambient noise from ocean surf increases. Our results are in line with the hypothesis that, as in the case of anthropogenic noise, natural ambient noise affects acoustic signalling in birds (Kirschel, Blumstein, Cohen et al. 2009; Davidson et al. 2017). We show that the masking effect of a natural low-frequency noise can affect vocalisations of animals that lack the capacity to develop vocalisations through auditory feedback. Higher dominant frequency may confer an adaptive advantage to coastal populations of tinkerbirds because they benefit from increased transmission of signals to intended receivers. Therefore, individuals with higher dominant frequency songs may have higher fitness at coastal sites. Low-frequency natural noise such as from ocean surf, rivers and waterfalls can have a profound effect on auditory communication, as shown in concave-eared torrent frog (*Amolops tormotus*), whose calls include ultrasound elements in their preferred habitat alongside fast-flowing streams (Feng et al. 2006). Support for such acoustic adaptation has also been demonstrated when comparing torrent frogs to other species living in different habitats (Goutte et al. 2018). Tinkerbirds are not restricted to such noisy environments, yet divergence in frequency appears to occur in spite of ongoing gene flow with adjacent inland populations.

The pressure imposed by ocean surf low-frequency noise may have strong effects on how species interact acoustically because of potential interference with their vocalisations in the frequency domain. The effects of low-frequency ambient noise are likely to have a stronger selective impact on species vocalising at lower frequency and especially in birds with limited vocal flexibility (Goodwin and Shriver 2011; Halfwerk et al. 2011), such as tinkerbirds, because of a possible inability to increase their frequency to improve communication with other individuals. In this study, *fischeri* is the species with the lowest dominant frequency and therefore may be subjected to a greater pressure by ocean surf. Yet, in contrast to findings for the other two species, the effect of distance from the coast on its frequency was not significant (Figure 3). In Kenya, it co-occurs with two other *Pogoniulus* tinkerbirds: *P. pusillus* and eastern green tinkerbird *P. simplex* (hereafter *simplex*), both of which sing at higher frequencies than *fischeri*, and *simplex* sings a trilled song not unlike that of *fischeri*. It is therefore possible that populations of *fischeri* are constrained to avoid the masking effect of low-frequency ocean surf sound by increasing their dominant frequency because an increased pitch would result in greater interference with its two competitors (e.g., Kirschel, Blumstein and Smith 2009). Indeed, an increase in dominant frequency in continental populations of *fischeri* could lead to song overlap in the frequency domain with its two congeners (Figure 4b). Stabilising selection might maintain *fischeri* song frequency at a level that best reduces the masking effects of surf sound while maintaining sufficient frequency differences between *fischeri* and other tinkerbird species. This is consistent with work in Asian barbet communities demonstrating they maintain dispersion in acoustic traits (Krishnan and Tamma 2016). Coastal *fischeri* sing a much faster trilled song than other forms of *P. bilineatus* (Nwankwo et al. 2018) and the rapid repetition of pulses might itself be an adaptation to its sound environment in coastal forests (Slabbekoorn and den Boer-visser 2006; Redondo et al. 2013). An alternative hypothesis is that *fischeri* song might have evolved by convergent

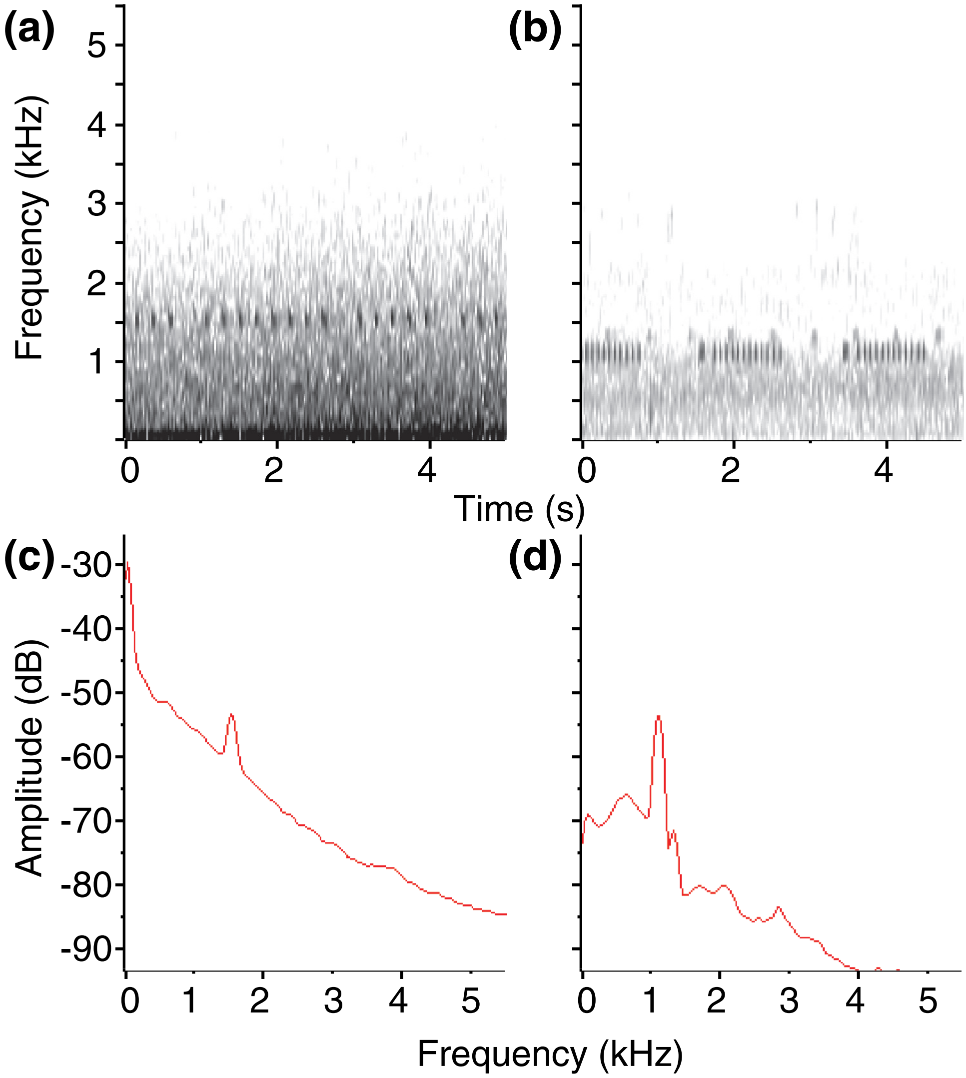

Figure 4. Illustration of the masking effect of ocean surf sound in spectrograms (a-b) and power spectra profiles (c-d) of *subsulphureus* song (left panels), and *pusillus* and *fischeri* singing together (right panels), with *subsulphureus* song recorded at 68 m and *pusillus* and *fischeri* songs recorded at 330 m from the shore.

character displacement to facilitate interspecific territoriality with *simplex* (e.g., Kirschel et al. 2019). However, further work is needed to investigate the extent to which *fischeri* song may also vary because of such interactions with its congeners.

The three species of tinkerbirds studied here are similar in body size, (Short and Horne 2002), and phenology, as they are all sedentary species. Hence, we do not expect tinkerbird song to vary because of such factors, except that the slightly larger body mass of *fischeri* corresponds with its lower frequency song compared to *subsulphureus* and *pusillus* (e.g. Kirschel, Zanti, et al. 2020). Other factors that may have the potential to affect tinkerbird vocalisations are vegetation (Bradbury and Vehrencamp 2011), seasonality of wind patterns, with the latter potentially affecting the movement of sea waves and therefore noise production (Jeffreys 1925), and interference of insect noise (Kirschel, Blumstein, Cohen, et al. 2009). However, sampling locations both in Western and Eastern Africa are characterised by dense vegetation, with tropical rain forest occurring in the west, and primarily coastal forest occurring at our field sites in the east. Therefore, we do not expect the two habitats to have marked structural differences that might affect tinkerbird song. Indeed, a study on transmission properties of tropical forest in Cameroon, including at a site (Kribi) included in the present study, did not find evidence of differences in transmission properties between forest and ecotone, with the latter consisting in forest patches within a savannah matrix (Slabbekoorn and Smith 2002b). We suggest the coastal forest in Kenya has intermediate vegetation structure between those habitats, in terms of canopy cover and height. Furthermore, habitat type is consistent throughout the range of distances considered, and habitat differences between individuals at coastal sites and those occupying territories further inland are unlikely to occur. Besides habitat, periodic variations in sea wave motion might influence surf sound. El Niño Southern Oscillation (ENSO) is a climatic phenomenon that impacts sea currents and consequently wind circulation, and has been shown to play an important part in determining climatic patterns in both Eastern and Western Africa (Camberlin et al. 2001). However, our expectation is that the tinkerbird response to surf sound is adaptive rather than a plastic response to seasonal fluctuations in ocean noise because as Piciformes they do not develop their songs using auditory feedback. As such, seasonal patterns of wind circulation that can in turn affect surf sound, are unlikely to have led to different selective pressure on tinkerbird vocalisations between populations in Eastern and Western Africa. Finally, regarding insect noise, we find unlikely that it has an effect on tinkerbird song, because insects emit higher frequency sounds (typically over 4 kHz) that are unlikely to overlap with tinkerbird songs (1–-1.5 kHz) (Kirschel, Blumstein, Cohen, et al. 2009; Kirschel et al. 2011).

Higher dominant frequency has been suggested to be a consequence of an increased song amplitude in non-passerines (Elemans et al. 2008; Nemeth and Brumm 2010; Nemeth et al. 2012), whereas this is not always the case in passerines, which present higher vocal flexibility (Zollinger et al. 2017). An increased amplitude can be an adaptation to noisy environments according to the Lombard effect, which occurs when frequency range of the vocalising animal and the background noise overlap (Brumm and Todt 2002). In our study, ocean surf sound widely overlaps with tinkerbirds song frequencies (Figure 4), therefore one possibility is that increased dominant frequency in tinkerbird song at coastal sites is a consequence of raised vocal amplitude. The Lombard effect is a common trait in many bird clades including passerines (Brumm and Todt 2002), Galliformes (Brumm et al. 2009) and even in Paleognathae species such as tinamous (Schuster et al. 2012). The ancestral nature of the Lombard effect suggests it occurs independently of the ontogeny of vocal learning in birds (Brumm et al. 2009; Brumm and Zollinger 2011) and increased frequencies in tinkerbird song might also be a consequence of increased vocal amplitude. This phenomenon has been observed in other birds that lack song learning (Schuster et al. 2012). However, we did not specifically test whether the increased dominant frequency occurs as a consequence of the Lombard effect in tinkerbirds, but our results highlight this as a compelling area for future investigations.

Singing higher-pitch songs in coastal sites may be an advantage in tinkerbirds, as higher frequency songs often represent a selected trait by females (Hasegawa and Arai 2016). Also, an increased pitch may result in an increased detectability by opposite-sex individuals. Assuming that song frequency is correlated with amplitude, increased frequency would result in a far-reaching signal which may further aid mate attraction. Similarly, in territorial contests, higher-pitch song may result in a larger active space (Brumm and Todt 2002) – a potential advantage in territorial birds like tinkerbirds. The transmission of high-frequency songs, however, has been shown to be attenuated in densely vegetated habitats (Wiley 2006). Therefore, high-pitch songs travel longer distances only if the increase in pitch is accompanied by an increase in song amplitude.

As the production of frequencies depends on the size of the syringeal membrane (Nowicky and Marler 1988), pitch has been shown in many birds to be negatively correlated with body size (Ryan and Brenowitz 1985; Brumm and Goymann 2017; Derryberry et al. 2018), even among conspecifics (Kirschel, Zanti, et al. 2020), whereas it does not seem to affect song amplitude (Brumm 2009). Hence, any relative advantage in terms of signal transmission may be counterbalanced by increased aggression from larger males, as higher frequency song may be interpreted as a sign of weakness (Kirschel, Zanti, et al. 2020). Ocean surf sound is a continuous noise whose pressure acts over evolutionary timescales on birdsong,; therefore, the trade-offs between the potential advantages of increased mate attraction and at the same time increased territorial response from other males may have had profound evolutionary implications in shaping tinkerbird acoustic signals.

In this paper, we show that tinkerbirds sing at a higher dominant frequency the closer they are to the coastline. We suggest that low-frequency noise from ocean surf imposes a selective pressure on tinkerbird acoustic signalling, and higher dominant frequency songs may be selected because they reduce the masking effect of ocean surf sound. This effect might be boosted if an increase in dominant frequency is accompanied by an increase in amplitude. We predict that an increase in dominant frequency will occur but caution that overlapping frequencies with related species might influence acoustic competition, as might occur in our study in *fischeri* where it coexists with *pusillus* and *simplex*. Our results show that natural ambient noise has a similar impact to anthropogenic noise even on birds that do not learn their songs, in line with the effects of natural ambient noise on oscine passerine vocalisations (Davidson et al. 2017). We believe that our results on birds that develop songs innately can be extrapolated in other contexts of background noise, including anthropogenic noise pollution, and therefore represent a baseline for further studies on the effect of background noise on bird song.

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Ethics approval

This project did not require ethics approval but all permits are listed below under consent to participate.

Consent to participate

Permits for research were obtained from the Cameroon Biodiversity Conservation Society, National Museums of Kenya, Kenya National Council for Science and Technology, Tanzania Wildlife Research Institute, and Tanzania Commission for Science and Technology.

Consent for publication

All authors consent to the publication

Disclosure statement

We declare no conflicts of interest

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Data availability statement

Supplementary material, raw data in this study and the code used in R are available on Figshare online repository (DOI: 10.6084/m9.figshare.12948320) https://figshare.com/articles/online_resource/Ambient_noise_from_ocean_surf_drives_frequency_shifts_in_non-passerine_bird_song/12948320.

Authors' contributions

ANGK conceived the project and designed it with DTB, ANGK performed fieldwork, MS analysed data, and MS and ANGK wrote the paper with contributions from DTB.

References

Amador A, Goller F, Mindlin GB. 2008. Frequency modulation during song in a suboscine does not require vocal muscles. J Neurophysiol. 99(5):2383–2389. doi:10.1152/jn.01002.2007.

Araya-Salas M. 2020. baRulho: quantifying habitat-induced degradation of (animal) acoustic signals in R. R package version 1.0.0.

Araya-Salas M, Smith-Vidaurre G, Webster M. 2019. Assessing the effect of sound file compression and background noise on measures of acoustic signal structure. Bioacoustics. 28(1):57–73. doi:10.1080/09524622.2017.1396498

Beckers GJL, Suthers RA, Ten Cate C. 2003. Mechanisms of frequency and amplitude modulation in ring dove song. J Exp Biol. 206(11):1833–1843. doi:10.1242/jeb.00364.

Bermúdez-Cuamatzin E, Ríos-Chelén AA, Gil D, Garcia CMÍ. 2009. Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? Behaviour. 146(9):1269–1286. doi:10.1163/156853909X423104.

Blumstein DT, Mennill DJ, Clemins P, Girod L, Yao K, Patricelli G, Deppe JL, Krakauer AH, Clark C, Cortopassi KA, et al. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. J Appl Ecol. 48 (3):758–767. doi:10.1111/j.1365-2664.2011.01993.x.

Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. 2nd ed. Sunderland (MA): Sinauer. doi:10.1086/669301.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9(2):378–400. doi: 10.32614/RJ-2017-066.

Brumm H, Naguib M. 2009. Environmental acoustics and the evolution of bird song. In: Naguib M, Zuberbuumlhler K, Clayton N, Janik V, editors. Advances in the study of behavior. Cambridge (MA): Academid Press; p. 1–33. https://doi.org/10.1016/S0065-3454(09)40001-9 .

Brumm H. 2009. Song amplitude and body size in birds. Behav Ecol Sociobiol. 63(8):1157–1165. doi:10.1007/s00265-009-0743-4.

Brumm H. 2013. Animal communication and noise. Vol. 2. Heidelberg, Berlin (Germany): Springer-Verlag.

Brumm H, Goymann W. 2017. On the natural history of duetting in White-browed Coucals: sex- and body-size-dependent differences in a collective vocal display. J Ornithol. 158(3):669–678. doi:10.1007/s10336-016-1429-0.

Brumm H, Schmidt R, Schrader L. 2009. Noise-dependent vocal plasticity in domestic fowl. Anim Behav. 78(3):741–746. doi:10.1016/j.anbehav.2009.07.004.

Brumm H, Slabbekoorn H. 2005. Acoustic communication in noise. Adv Study Behav. 35 (5):151–209. doi:10.1016/S0065-3454(05)35004-2.

Brumm H, Slater PJB. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behav Ecol Sociobiol. 60(4):475–481. doi:10.1007/s00265-006-0188-y.

Brumm H, Todt D. 2002. Noise-dependent song amplitude regulation in a territorial songbird. Anim Behav. 63(5):891–897. doi:10.1006/anbe.2001.1968.

Brumm H, Zollinger A. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour. 148(11–13):1173–1198. doi:10.1163/000579511X605759.

Brumm H, Zollinger SA, Niemelä PT, Sprau P. 2017. Measurement artefacts lead to false positives in the study of birdsong in noise. Methods Ecol Evol. 8(11):1617–1625. doi:10.1111/2041-210X.12766.

Camberlin P, Janicot S, Poccard I. 2001. Seasonality and atmospheric dynamics of the teleconnection between African rainfall and tropical sea-surface temperature: atlantic vs. ENSO. Int J Climatol. 21(8):973–1005. doi:10.1002/joc.673.

Catchpole CK, Slater PJB. 1995. Bird song: biological themes and variation. Cambridge (UK): Cambridge University Press.

Center for Conservation Bioacoustics. 2019. Raven Pro: interactive sound analysis software (Version 1.6) [Computer software]. Ithaca (NY): The Cornell Lab of Ornithology. Available from: http://ravensoundsoftware.com/ .

Daniels FB. 1952. Acoustical energy generated by the ocean waves. J Acoust Soc Am. 24(1):83. doi:10.1121/1.1906855.

Davidson BM, Antonova G, Dlott H, Barber JR, Francis CD. 2017. Natural and anthropogenic sounds reduce song performance: insights from two emberizid species. Behav Ecol. 28 (4):974–982. doi:10.1093/beheco/arx036.

de Tolentino VCM, Baesse CQ, de Melo C. 2018. Dominant frequency of songs in tropical bird species is higher in sites with high noise pollution. Environ Pollut. 235:983–992. doi:10.1016/j.envpol.2018.01.045.

Deoniziak K, Osiejuk TS. 2016. Disentangling relations among repertoire size, song rate, signal redundancy and ambient noise level in European songbird. Ethology. 122(9):734–744. doi:10.1111/eth.12520.

Deoniziak K, Osiejuk TS. 2019. Habitat-related differences in song structure and complexity in a songbird with a large repertoire. BMC Ecol. 19(1):1–11. doi:10.1186/s12898-019-0255-7.

Derryberry EP, Seddon N, Derryberry GE, Claramunt S, Seeholzer GF, Brumfield RT, Tobias JA. 2018. Ecological drivers of song evolution in birds: disentangling the effects of habitat and morphology. Ecol Evol. 8(3):1890–1905. doi:10.1002/ece3.3760.

Dominoni DM, Greif S, Nemeth E, Brumm H. 2016. Airport noise predicts song timing of European birds. Ecol Evol. 6(17):6151–6159. doi:10.1002/ece3.2357.

Douglas HD, Conner WE. 1999. Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. Naturwissenschaften. 86(5):228–230. doi:10.1007/s001140050603.

Dowsett-Lemaire F. 1988. Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. Rev Ecol. 43:251–285.

Elemans CPH, Zaccarelli R, Herzel H. 2008. Biomechanics and control of vocalization in a non-songbird. J R Soc Interface. 5(24):691–703. doi:10.1098/rsif.2007.1237.

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. Am Nat. 139(March): S125–S153. doi:10.1086/285308.

Feng AS, Narins PM, Xu CH, Lin WY, Yu ZL, Qiu Q, Xu ZM, Shen JX. 2006. Ultrasonic communication in frogs. Nature. 440(7082):333–336. doi:10.1038/nature04416.

Fox J, Weisberg S. 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. J Stat Softw. 87:1–27. doi:10.18637/jss.v087.i09.

Francis CD, Ortega CP, Cruz A. 2011. Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biol Lett. 7(6):850–852. doi:10.1098/rsbl.2011.0359.

Gentry KE, McKenna MF, Luther DA. 2018. Evidence of suboscine song plasticity in response to traffic noise fluctuations and temporary road closures. Bioacoustics. 27(2):165–181. doi:10.1080/09524622.2017.1303645.

Godschalk SKB. 1985. Feeding behaviour of avian dispersers of mistletoe fruit in the Loskop Dam nature reserve, South Africa. South African J Zool. 20(3):136–146. doi:10.1080/02541858.1985.11447926.

Goodwin SE, Shriver WG. 2011. Effects of traffic noise on occupancy patterns of forest birds. Conserv Biol. 25(2):406–411. doi:10.1111/j.1523-1739.2010.01602.x.

Gossard EE, Hooke WH. 1975. Waves in the atmosphere: atmospheric infrasound and gravity waves - their generation and propagations. Amsterdam (NL): Elsevier.

Goutte S, Dubois A, Howard SD, Márquez R, Rowley JJL, Dehling JM, Grandcolas P, Xiong RC, Legendre F. 2018. How the environment shapes animal signals: a test of the acoustic adaptation hypothesis in frogs. J Evol Biol. 31(1):148–158. doi:10.1111/jeb.13210.

Halfwerk W, Bot S, Buikx J, Van Der Velde M, Komdeur J, Ten Cate C, Slabbekoorn H. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proc Natl Acad Sci U S A. 108 (35):14549–14554. doi:10.1073/pnas.1109091108.

Halfwerk W, Lohr B, Slabbekoorn H. 2018. Impact of man-made sound on birds and their songs. In: Effects od anthropogenic noise on animals. New York (NY): Springer; p. 209–242.

Halfwerk W, Ryan MJ, Wilson PS. 2016. Wind- and rain-induced vibrations impose different selection pressures on multimodal signaling. Am Nat. 188(3):279–288. doi:10.1086/687519.

Halfwerk W, Slabbekoorn H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. Anim Behav. 78(6):1301–1307. doi:10.1016/j.anbehav.2009.09.015.

Harting F. 2019. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.1. https://CRAN.R-project.org/package=DHARMa .

Hasegawa M, Arai E. 2016. Female attraction to higher pitched male enticement calls in Barn Swallows. Ethology. 122(5):430–441. doi:10.1111/eth.12492.

Hu Y, Cardoso GC. 2010. Which birds adjust the frequency of vocalizations in urban noise? Anim Behav. 79(4):863–867. doi:10.1016/j.anbehav.2009.12.036.

Jeffreys H. 1925. On the formation of water waves by wind. Proc R Soc A. 107(742):189–206. doi:10.1098/rspa.1925.0015.

Kirschel ANG, Blumstein DT, Cohen RE, Buermann W, Smith TB, Slabbekoorn H. 2009. Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. Behav Ecol. 20(5):1089–1095. doi:10.1093/beheco/arp101.

Kirschel ANG, Blumstein DT, Smith TB. 2009. Character displacement of song and morphology in African tinkerbirds. Proc Natl Acad Sci U S A. 106(20):8256–8261. doi:10.1073/pnas.0810124106.

Kirschel ANG, Nwankwo EC, Seal N, Grether GF. 2020. Time spent together and time spent apart affect song, feather colour and range overlap in tinkerbirds. Biol J Linn Soc. 129(2):439–458. doi:10.1093/biolinnean/blz191.

Kirschel ANG, Seddon N, Tobias JA. 2019. Range-wide spatial mapping reveals convergent character displacement of bird song. Proc R Soc B Biol Sci. 286(1902):17–19. doi:10.1098/rspb.2019.0443.

Kirschel ANG, Slabbekoorn H, Blumstein DT, Cohen RE, De Kort SR, Buermann W, Smith TB. 2011. Testing alternative hypotheses for evolutionary diversification in an African songbird: rainforest refugia versus ecological gradients. Evolution (N Y). 65(11):3162–3174. doi:10.1111/j.1558-5646.2011.01386.x.

Kirschel ANG, Zanti Z, Harlow ZT, Vallejo EE, Cody ML, Taylor CE. 2020. Females don't always sing in response to male song, but when they do, they sing to males with higher-pitched songs. Anim Behav. 166:129–138. doi:10.1016/j.anbehav.2020.06.024.

Krishnan A, Tamma K. 2016. Divergent morphological and acoustic traits in sympatric communities of Asian barbets. R Soc Open Sci. 3(8):160117. doi:10.1098/rsos.160117.

Kroodsma DE. 1982. Acoustic communication in birds. New York: Academid Press.

LaZerte SE, Otter KA, Slabbekoorn H. 2017. Mountain chickadees adjust songs, calls and chorus composition with increasing ambient and experimental anthropogenic noise. Urban Ecosyst. 20 (5):989–1000. doi:10.1007/s11252-017-0652-7.

LaZerte SE, Slabbekoorn H, Otter KA. 2016. Learning to cope: vocal adjustment to urban noise is correlated with prior experience in black-capped chickadees. Proc R Soc B Biol Sci. 283 (1833):20161058. doi:10.1098/rspb.2016.1058.

Lengagne T, Aubin T, Lauga J, Jouventin P. 1999. How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? Proc R Soc B Biol Sci. 266(1429):1623–1628. doi:10.1098/rspb.1999.0824.

Lengagne T, Slater PJB. 2002. The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. Proc R Soc B Biol Sci. 269(1505):2121–2125. doi:10.1098/rspb.2002.2115.

Lowther PE, Douglas HD III, Gratto-Trevor CL. 2001. Willet: *catoptrophorus semipalmatus*. In: Poole EA, Gill F, editors. Birds of North America. Philadelphia (PA, USA): BNA, Inc; p. 1–32.

Luther DA, Phillips J, Derryberry EP. 2016. Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. Behav Ecol. 27(1):332–340. doi:10.1093/beheco/arv162.

Mendes S, Colino-Rabanal VJ, Peris SJ. 2011. Bird song variations along an urban gradient: the case of the European blackbird (*Turdus merula*). Landsc Urban Plan. 99(1):51–57. doi:10.1016/j.landurbplan.2010.08.013.

Moseley DL, Derryberry GE, Phillips JN, Danner JE, Danner RM, Luther DA, Derryberry EP. 2018. Acoustic adaptation to city noise through vocal learning by a songbird. Proc R Soc B Biol Sci. 285(1888):20181356. doi:10.1098/rspb.2018.1356.

Naguib M, Riebel K. 2014. Singing in space and time: the biology of birdsong. In: Biocommunication of animals. Dordrecht: Springer; p. 233–247.

Naguib M, Wiley RH. 2001. Review: estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Anim Behav. 62(5):825–837. doi:10.1006/anbe.2001.1860.

Nemeth E, Brumm H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Anim Behav. 78(3):637–641. doi:10.1016/j.anbehav.2009.06.016.

Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: are urban songs adaptive? Am Nat. 176(4):465–475. doi:10.1086/656275.

Nemeth E, Zollinger SA, Brumm H. 2012. Effect sizes and the integrative understanding of urban bird song: (A reply to Slabbekoorn et al. Am Nat. 180(1):146–152. doi:10.1086/665994.

Nottebohm F. 1972. The origins of vocal learning. Am Nat. 106(947):116–140. doi:10.1086/282756.

Nowicky S, Marler P. 1988. How do birds sing? Music Percept. 5(4):391–426. doi:10.2307/40285408.

Nwankwo EC, Mortega KG, Karageorgos A, Ogolowa BO, Papagregoriou G, Grether GF, Monadjem A, Kirschel ANG. 2019. Rampant introgressive hybridization in *Pogoniulus* tinkerbirds (Piciformes: Lybiidae) despite millions of years of divergence. Biol J Linn Soc. 127(1):125–142. doi:10.1093/biolinnean/blz018.

Nwankwo EC, Pallari CT, Hadjioannou L, Ioannou A, Mulwa RK, Kirschel ANG. 2018. Rapid song divergence leads to discordance between genetic distance and phenotypic characters important in reproductive isolation. Ecol Evol. 8(1):716–731. doi:10.1002/ece3.3673.

Osmanski MS, Dooling RJ. 2009. The effect of altered auditory feedback on control of vocal production in budgerigars (*Melopsittacus undulatus*). J Acoust Soc Am. 126(2):911–919. doi:10.1121/1.3158928.

Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk. 123(3):639. doi:10.1093/auk/123.3.639.

Proppe DS, Avey MT, Hoeschele M, Moscicki MK, Farrell T, St Clair CC, Sturdy CB. 2012. Black-capped chickadees *Poecile atricapillus* sing at higher pitches with elevated anthropogenic noise, but not with decreasing canopy cover. J Avian Biol. 43(4):325–332. doi:10.1111/j.1600-048X.2012.05640.x.

Proppe DS, Sturdy CB, St. Clair CC. 2011. Flexibility in animal signals facilitates adaptation to rapidly changing environments. PLoS One. 6(9):1–4. doi:10.1371/journal.pone.0025413.

Redondo P, Barrantes G, Sandoval L. 2013. Urban noise influences vocalization structure in the House Wren *Troglodytes aedon*. Ibis (Lond 1859). 155(3):621–625. doi:10.1111/ibi.12053.

Ríos-Chelén AA, McDonald AN, Berger A, Perry AC, Krakauer AH, Patricelli GL. 2017. Do birds vocalize at higher pitch in noise, or is it a matter of measurement? Behav Ecol Sociobiol. 71(1):1–12. doi:10.1007/s00265-016-2243-7.

Ríos-Chelén AA, Salaberria C, Barbosa I, Macías Garcia C, Gil D. 2012. The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. J Evol Biol. 25(11):2171–2180. doi:10.1111/j.1420-9101.2012.02597.x.

Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. Am Nat. 126(1):87–100. doi:10.1086/284398.

Saranathan V, Hamilton D, Powell GVN, Kroodsma DE, Prum RO. 2007. Genetic evidence supports song learning in the three-wattled bellbird *Procnias tricarunculata* (Cotingidae). Mol Ecol. 16(17):3689–3702. doi:10.1111/j.1365-294X.2007.03415.x.

Scarl JC, Bradbury JW. 2009. Rapid vocal convergence in an Australian cockatoo, the galah *Eolophus roseicapillus*. Anim Behav. 77(5):1019–1026. doi:10.1016/j.anbehav.2008.11.024.

Schuster S, Zollinger SA, Lesku JA, Brumm H. 2012. On the evolution of noise-dependent vocal plasticity in birds. Biol Lett. 8(6):913–916. doi:10.1098/rsbl.2012.0676.

Seddon N. 2005. Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. Evolution (N Y). 59(1):200–215. doi:10.1111/j.0014-3820.2005.tb00906.x.

Short LL, Horne JFM. 2002. Family Capitonidae (barbets). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, editors. Handbook of the birds of the world (Vol. 7). Barcelona: Lynx Edicions, Barcelona, Spain; p. 140–219.

Short LL, Horne JFM. 2001. Toucans, barbets and honeyguides. New York (NY): Oxford University Press.

Sierro J, Schloesing E, Pavón I, Gil D. 2017. European blackbirds exposed to aircraft noise advance their chorus, modify their song and spend more time singing. Front Ecol Evol. 5(JUN):1–13. doi:10.3389/fevo.2017.00068.

Slabbekoorn H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim Behav. 85(5):1089–1099. doi:10.1016/j.anbehav.2013.01.021.

Slabbekoorn H, den Boer-visser A. 2006. Cities Change the Songs of Birds. Curr Biol. 16 (23):2326–2331. doi:10.1016/j.cub.2006.10.008.

Slabbekoorn H, Ripmeester EAP. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Mol Ecol. 17(1):72–83. doi:10.1111/j.1365-294X.2007.03487.x.

Slabbekoorn H, Smith TB. 2002a. Bird song, ecology and speciation. Philos Trans R Soc B Biol Sci. 357(1420):493–503. doi:10.1098/rstb.2001.1056.

Slabbekoorn H, Smith TB. 2002b. Habitat-dependent song divergence in the Little Greenbul: analysis of environmental selection pressures on acoustic signals. Evolution (N Y). 9 (56):1849–1858. doi:10.1111/j.0014-3820.2002.tb00199.x.

Swaddle JP, Francis CD, Barber JR, Cooper CB, Kyba CCM, Dominoni DM, Shannon G, Aschehoug E, Goodwin SE, Kawahara AY, et al. 2015. A framework to assess evolutionary responses to anthropogenic light and sound. Trends Ecol Evol. 30(9):550–560. doi:10.1016/j.tree.2015.06.009.

Touchton JM, Seddon N, Tobias JA. 2014. Captive rearing experiments confirm song development without learning in a tracheophone suboscine bird. PLoS One. 9(4). doi:10.1371/journal.pone.0095746.

Western C, Douglas HD, Carolina N. 1998. Response of Eastern Willets (*Catoptrophorus s . semipalmatus*) to vocalizations of Eastern and Western (C. s. inornatus) Willets. Auk. 115 (2):514–518. doi:10.2307/4089216.

Wiley RH. 2006. Signal detection and animal communication. Adv Study Behav. 36:217–247. doi:10.1016/S0065-3454(06)36005-6.

Zollinger SA, Brumm H. 2011. The Lombard effect. Curr Biol. 21(16):R614–R615. doi:10.1016/j.cub.2011.06.003.

Zollinger SA, Podos J, Nemeth E, Goller F, Brumm H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. Anim Behav. 84:1–9. doi:10.1016/j.anbehav.2012.04.026.

Zollinger SA, Slater PJB, Nemeth E, Brumm H. 2017. Higher songs of city birds may not be an individual response to noise. Proc R Soc B Biol Sci. 284(1860):20170602. doi:10.1098/rspb.2017.0602.