

1 **Ambient noise from ocean surf drives frequency shifts in non-passerine bird song**

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14

15

16 **Abstract**

17 Effective communication in birds is often hampered by background noise, with many recent
18 studies focusing on the effect of anthropogenic noise on passerine bird song. Continuous low-
19 frequency natural noise is predicted to drive changes in both frequency and temporal
20 patterning of bird vocalizations, but the extent to which these effects may also affect birds
21 that lack vocal learning is not yet fully understood. Here we use a gradient of exposure to
22 natural low-frequency noise to assess whether it exerts selective pressure on vocalizations in
23 a species whose songs are innate. We tested whether three species of *Pogoniulus* tinkerbirds
24 adapt their song when exposed to a source of continuous low-frequency noise from ocean
25 surf. We show that dominant frequency increases the closer birds are to the coast in all the
26 three species, and in line with higher noise levels, indicating that ocean surf sound may apply
27 a selective pressure on tinkerbird songs. As a consequence, tinkerbirds adapt their songs with
28 an increase in frequency to avoid the masking effect due to overlapping frequencies with
29 ambient noise, therefore improving long-range communication with intended receivers. Our
30 study provides for the first time, compelling evidence that natural ambient noise affects
31 vocalizations in birds whose songs are developed innately. We believe that our results can
32 also be extrapolated in the context of anthropogenic noise pollution, hence providing a
33 baseline for the study of the effects of low-frequency ambient noise on birds that lack vocal
34 learning.

35 **Significance Statement**

36 Birdsong is constantly under selection as it mediates key interactions such as mate attraction,
37 competition with same-sex individuals for reproduction and competition with heterospecifics
38 for space-related resources. Any phenomenon that interferes with communication can
39 therefore have a profound impact on individual fitness. Passerines are more likely to avoid

40 the masking effect of background noise because of their higher vocal flexibility. Many non-
41 passerine species lacking such flexibility might therefore be more vulnerable to the negative
42 effects on their fitness of exposure to low-frequency background noise. Species incapable of
43 adapting their signals to background noise are predicted to disappear from noisy areas.
44 Despite this, we show that species that lack song learning may show an adaptive response to
45 natural noise which may develop over evolutionary timescales.

46

47 **Introduction**

48 Many species rely on acoustic communication to accomplish functions that are crucial for
49 their survival (Bradbury and Vehrencamp 2011). Bird song, for instance, has been shown to
50 mediate behaviours involved in mate attraction, competition for partners, food and space
51 (Catchpole and Slater 2008; Naguib and Riebel 2014); even though it may also function to
52 coordinate group movements and to warn other individuals against potential threats (Naguib
53 and Wiley 2001; Bradbury and Vehrencamp 2011; Halfwerk et al. 2018). An effective signal
54 transfer is therefore essential to ensure the prompt behavioural response of the receiver.

55 The transfer of clear signals might be hampered by the sound transmission properties
56 of the environment, which may degrade signals (Brumm and Naguib 2009), or by
57 interference from environmental noise (Brumm and Slabbekoorn 2005; Blumstein et al.
58 2011). Under the latter scenario, sounds similar in frequency and amplitude can have a
59 masking effect and potentially lead to the transmission of incomplete or incorrect information
60 (Slabbekoorn 2013). Such effects have a strong effect on vocal behaviour of birds (Patricelli
61 and Blickley 2006; Slabbekoorn 2013). Indeed, experiments have shown birds in one
62 environment with a specific ambient noise profile respond less to songs adapted to different
63 ambient noise profiles than to those adapted to similar ambient noise profiles (Kirschel et al.
64 2011). Therefore, loud and continuous background noise impose strong selective pressures on

65 bird song to increase its effectiveness in noisy environments (Slabbekoorn and Smith 2002;
66 Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Slabbekoorn and den Boer-
67 Visser 2006; Slabbekoorn and Ripmeester 2008; Halfwerk and Slabbekoorn 2009; Nemeth
68 and Brumm 2010).

69 Birds react to low frequency ambient noise pressure in different ways (Brumm and
70 Slabbekoorn 2005; Swaddle et al. 2015). Some have been shown to increase their minimum
71 frequency (Slabbekoorn and den Boer-Visser 2006; Nemeth and Brumm 2009, 2010; Hu and
72 Cardoso 2010; Mendes et al. 2011; Ríos-Chelén et al. 2012), maximum frequency (Francis et
73 al. 2011; Mendes et al. 2011) and others their dominant frequency (Nemeth and Brumm
74 2009; Hu and Cardoso 2010; Proppe et al. 2011, 2012; Lazerte et al. 2016; Luther et al. 2016;
75 LaZerte et al. 2017; Tolentino et al. 2018) in response to background noise. Increases in
76 frequency may, however, be a side effect of singing at higher amplitude in noisy
77 environments (Nemeth and Brumm 2010) - the Lombard Effect (Brumm and Zollinger 2011;
78 Zollinger and Brumm 2011) - as amplitude and song frequency are often correlated (Beckers
79 et al. 2003; Amador et al. 2008; Zollinger et al. 2012). Other adaptations to low-frequency
80 ambient noise include increasing signal redundancy (Brumm and Slater 2006; Deoniziak and
81 Osiejuk 2016), singing more often (Deoniziak and Osiejuk 2019), for longer periods (Brumm
82 and Slater 2006; Nemeth and Brumm 2009; Sierro et al. 2017) or at specific time intervals
83 (Dominoni et al. 2016).

84 Changes in vocal parameters can result from different mechanisms, for instance,
85 response to background noise might be plastic, as found in House Finches (*Carpodacus*
86 *mexicanus*) (Bermúdez-Cuamatzin et al. 2009), or learned, as demonstrated in Black-capped
87 chickadees (*Poecile atricapillus*) (Lazerte et al. 2016) and White-crowned sparrows
88 (*Zonotrichia leucophrys*) (Moseley et al. 2018). Shifts in signal design might also arise
89 because selection may favor individuals that minimize the masking effect of ambient noise

90 (Slabbekoorn and Smith 2002; Kirschel et al. 2009a, 2011). This scenario is compatible with
91 the song developing by sensory drive (Endler 1992), a mechanism which appears to have
92 shaped acoustic signals of many Neotropical suboscines (Seddon 2005) that lack song
93 learning capabilities (Touchton et al. 2014).

94 Most studies on the effects of noise on acoustic communication have addressed this
95 issue by looking at the effects of anthropogenic noise pollution. However, natural sources of
96 noise may have similar masking effects on animal signalling (Davidson et al. 2017; Goutte et
97 al. 2018). For instance, Halfwerk et al (2016) show multimodal communication between male
98 Tungara frogs (*Physalaemus pustulosus*) was hindered when geophonic noise from windy
99 and rainy conditions was simulated. Other studies on birds and other taxa have also shown an
100 effect of natural background noise on communication (Lengagne et al. 1999; Lengagne and
101 Slater 2002; Brumm and Slater 2006; Feng et al. 2006; Kirschel et al. 2009a; Davidson et al.
102 2017). Therefore, natural ambient noise is likely to be as impactful as anthropogenic noise
103 and with such noise present over evolutionary timescales it is likely to have evolutionary
104 implications for acoustic communication (Davidson et al. 2017).

105 To date, the study of the effects of ambient noise on bird signalling has focused
106 mostly on oscine passerines that learn their songs by way of auditory feedback (Hu and
107 Cardoso 2010; Ríos-Chelén et al. 2012). By contrast, there is scant information on how taxa
108 that lack vocal learning, such as suboscines and many non-passerines birds, cope with high
109 background noise levels (Gentry et al. 2018; Tolentino et al. 2018). Studies on non-passerines
110 include those on King penguins (*Aptenodytes*) (Lengagne et al. 1999) and Tawny owls
111 (Lengagne and Slater 2002). In both cases, responses to increased ambient noise were in
112 temporal patterning of their vocalizations. King penguins increased both the number of calls
113 and syllables per call emitted under strong winds, whereas Tawny owls reduced call rates
114 under rainy conditions because the interference of rain noise increased the unreliability of the

115 information conveyed in their calls. Hu and Cardoso (2010) did document changes in the
116 frequency domain in response to anthropogenic noise in a non-passerine by observing an
117 increase in minimum frequency in urban rainbow lorikeets (*Tricoglossus haematodus*) and
118 eastern rosellas (*Platycercus eximius*), two Psittaculidae (Order: Psittaciformes). However,
119 parrots, like hummingbirds and oscine passerines, are capable of vocal learning (Nottebohm
120 1972; Kroodsma 1982; Saranathan et al. 2007; Catchpole and Slater 2008) and therefore may
121 respond plastically to increased background noise levels (Osmanski and Dooling 2009; Scarl
122 and Bradbury 2009). Although birds not capable of learning such as suboscines and many
123 non-passerines may be more vulnerable to the effects of increased background noise given
124 their inability to adapt their signals (Ríos-Chelén et al. 2012), little is known about the
125 mechanisms that ensure efficient communication under noisy conditions in such taxa.

126 Here, we investigate whether *Pogoniulus* tinkerbirds (Family: Lybiidae; Order:
127 Piciformes) might adapt the frequency of their songs in response to increased geophonic
128 ambient noise from ocean surf. Tinkerbirds emit a simple, single pitch, stereotyped song that
129 develops innately (Kirschel et al. 2009a, 2020; Nwankwo et al. 2018). Because of the
130 absence of auditory feedback in song development, adaptation to noisy environments is
131 unlikely to involve a learned or plastic response. Instead, any variation in tinkerbird song that
132 would minimize the masking effect of noise may reflect an adaptive change. Hence, our
133 study specifically addresses whether there could be a selective pressure on tinkerbird song of
134 low frequency surf sound by focusing on species whose songs are innately developed.
135 Previous work has found evidence for character displacement in tinkerbird song frequency
136 when two species coexist at high densities, consistent with a role of competitive or
137 reproductive interference of songs of similar frequencies (Kirschel et al. 2009b, 2020). We
138 test whether yellow-throated (*Pogoniulus subsulphureus*), red-fronted (*P. pusillus*) and the
139 coastal subspecies of yellow-rumped tinkerbird (*P. bilineatus fischeri*) adjust their song along

140 a gradient of exposure to low-frequency ambient noise emanating from ocean surf in their
141 coastal populations. In the case of *P. subsulphureus*, we also measure local ambient noise to
142 test for a gradient in noise levels with distance and whether there is a direct relationship of
143 low frequency surf sound and song frequency.

144

145 **Methods**

146 **Study Species**

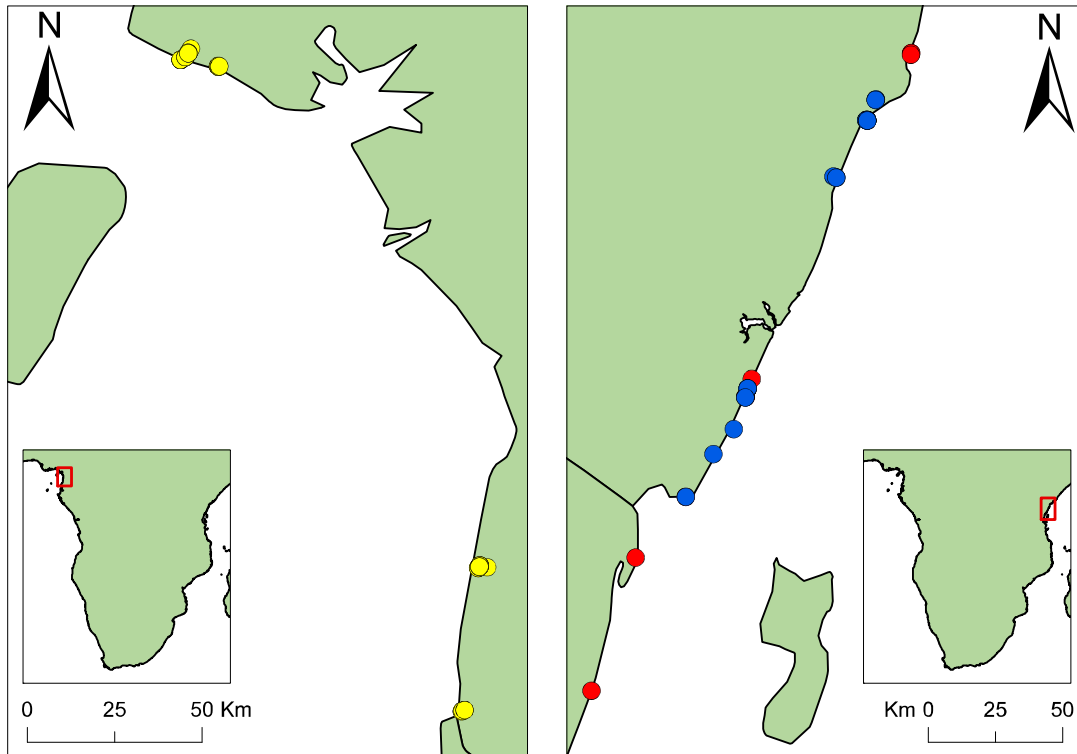
147 *Pogoniulus* tinkerbirds are barbets (Family: Lybiidae) that are widely distributed throughout
148 Sub-Saharan Africa. They are mostly frugivorous, feeding mainly on mistletoe, even though
149 they also take small invertebrates (Godschalk 1985; Dowsett-Lemaire 1988; Short and Horne
150 2001). *P. subsulphureus* (hereafter *subsulphureus*) strictly inhabits tropical lowland
151 rainforests in Central and Western Africa (Short and Horne 2002; Kirschel et al. 2020),
152 whereas *P. pusillus* (hereafter *pusillus*) occupy savanna woodland and secondary forest
153 below 2000 meters. On the other hand, *P. b. fischeri* (hereafter *fischeri*) only occurs in coastal
154 forests in southern Kenya and on the island of Zanzibar (Nwankwo et al. 2018).

155

156 **Song Collection and Acoustical Analysis**

157 We obtained recordings of *P. subsulphureus*, *P. pusillus* and *P. b. fischeri* from a total of 15
158 coastal locations in Cameroon and Kenya within 4 km from the shore (Fig.1). Fifty ambient
159 noise recordings were obtained from four locations in Cameroon by taking 1-minute long
160 recordings every hour from 7:00 to 12:00, holding the microphone horizontally every 10
161 seconds in each of the four cardinal direction (North, South, East, West) and then vertically
162 upwards, as described in Kirschel et al. (2009a). Ambient noise and *subsulphureus* songs
163 were recorded using a Marantz PMD670 a Sennheiser ME67, while *pusillus* and *fischeri*

164 songs were recorded with a Marantz PMD661 recorder with a MKH8050 or MKH8020
165 microphone, the latter housed in a Telinga parabolic reflector.
166



167
168 **Fig. 1** Map of recording localities in Cameroon (left) and Kenya (right). Coloured points
169 represent recording locations of *P. subsulphureus* (yellow), *P. pusillus* (red), and *P. b.*
170 *fischeri* (blue).

171
172 Recordings were saved as WAV or MP3 files and imported into Raven Pro 1.6
173 (Center for Conservation Bioacoustics 2019), in which songs were measured using its built-in
174 automated energy detectors. Target signal parameters were set as follow: minimum and
175 maximum frequencies spanned from 800 to 1700 Hz according to the species, minimum
176 duration was 0.03 s and maximum duration 0.3; minimum separation was set to 0.01 s for
177 *fischeri*, 0.05 s for *subsulphureus* and 0.25 for *pusillus*. The signal to noise ratio (SNR)

178 threshold was set in order to detect the maximum number of notes and varied depending on
179 the background noise levels on the recording. Most of the detections were obtained setting
180 the SNR above the threshold of 10-20 dB. We chose this instead of a manual-measurement
181 approach since the latter can lead to biased measurements (Brumm et al. 2017; Ríos-Chelén
182 et al. 2017). Raven provided peak frequency measurements from the spectrogram view (DFT
183 size: 4096; Window: Hanning, 3 dB; overlap: 50) and we obtained the dominant frequency
184 by calculating the mean from peak frequency values of all notes detected on each recording.

185 From the 50 ambient noise recordings, six were removed because of loud
186 anthropogenic traffic noise in the background and another was excluded because of loud
187 stream waterfall noise, both of obscured natural surf sound. From the remaining recordings,
188 we selected and merged together five high quality 5 s intervals per direction. In one instance
189 we included just the four 5 s intervals from cardinal directions, because the vertical recording
190 was beset by mechanical interference. Each 25 s song cut was then imported into R and the
191 ambient noise amplitude (dBA) at 1 kHz was calculated using the noise profile function
192 provided in the baRulho R package (Araya-Salas 2020). Subsequently, we used amplitude at
193 1 kHz (a measure of low frequency noise) as covariate in statistical models.

194 It was not possible to record data blind because our study was specifically focused on
195 tinkerbirds. While *subsulphureus* in Cameroon was sampled with this specific question in
196 mind, sampling of *pusillus* and *fischeri* was performed as part of parallel studies on song
197 variation (e.g., Nwankwo et al. 2018).

198

199 **Spatial Distance Calculation**

200 GPS coordinates of singing tinkerbirds and ambient noise recorded in the field were obtained
201 using a Garmin GPSMap. We imported the coordinates into Google Earth Pro and calculated

202 the closest distance from each recording location to the coastline using its built-in measuring
203 tool.

204

205 **Statistical Analysis**

206 To test whether ocean surf sound affects tinkerbird song, we measured the effect of distance
207 from the coast on dominant frequency of *subsulphureus*, *pusillus* and *fischeri* songs. This
208 effect was measured within 4 km from the coast as ambient noise recordings were collected
209 within that range and songs of birds further from the coast are likely influenced by other
210 factors, including elevation (Kirschel et al. 2009b). We assumed that, if ocean surf sound has
211 an effect on their song, dominant frequency would decrease as the distance from the coast
212 increases. For the coastal population of *subsulphureus* in Cameroon, for which ambient noise
213 recordings were also available, we tested whether dominant frequency increases with
214 background noise amplitude measured at 1 kHz, and also whether ambient noise (1 kHz) also
215 decreases with increased distance from the coast.

216 We fitted Gaussian generalized linear mixed models (GLMMs) in the glmmTMB R
217 package (Brooks et al. 2017) using log-transformed dominant frequency of *subsulphureus*,
218 *pusillus* and *fischeri* as response variables in three separate models and including log-distance
219 from the shore as a fixed factor. Bird ID nested in location were used as random factors to
220 account for individual variation as well as variation among field sites. In the *subsulphureus*
221 model, we also added ambient noise amplitude (measured at 1 kHz) of the closest ambient
222 noise recording as fixed factor. We then measured the effect of distance from the coast (log-
223 transformed) on ambient noise amplitude (1 kHz) in Cameroon coastal sites using the latter
224 as response variable and location as random effect. *subsulphureus* models were selected
225 according to the lowest corrected Akaike Information Criterion score. Assumptions of all
226 models were validated using the functions provided in DHARMA (Harting 2019).

227

228 **Results**

229 We obtained 86 recordings (39 *subsulphureus*, 21 *pusillus* and 26 *fischeri*) from a total of 65
230 individuals (31 *subsulphureus*, 16 *pusillus* and 18 *fischeri*) in our coastal sites in Cameroon
231 and Kenya (Fig.1) within 4 km. Of these, 2 were sourced from Xenocanto ([https://xeno-](https://xenocanto.org)
232 [canto.org](https://xenocanto.org)), respectively 1 for *pusillus* and 1 for *fischeri*. We found a significant negative
233 effect of distance from the coast (within 4 km) on dominant frequency (log-transformed) in
234 *subsulphureus*, *pusillus* and in *fischeri* (Fig 2, Table 1). *subsulphureus* model with both area
235 distance from the coast and ambient noise (1kHz) was not selected because presented high
236 AICc scores (Table S1).

237

238 **Table 1** Best fit Gaussian generalized linear mixed models output showing the relationship
239 between (log) dominant frequency and (log) distance from the coast for *subsulphureus*
240 (AICc: -138.24) (1), *pusillus* (2), *fischeri* (3) as well as relationship between surf sound
241 ambient noise and distance from the coast in Cameroon (4) and between *subsulphureus*
242 dominant frequency and ocean surf sound (5). Estimates and their lower (LCL) and upper
243 (UCL) confidence limits are presented.

244

| | Estimate | LCL | UCL | z | p |
|--------------------------------|----------|-------|-------|-------|--------|
| 1) Response: | | | | | |
| <i>P. subsulphureus</i> | | | | | |
| dominant frequency | | | | | |
| Intercept | 7.24 | 7.22 | 7.26 | 778.4 | <0.001 |
| (log) distance | -0.012 | -0.02 | -0.07 | -3.2 | 0.001 |
| 2) Response: | | | | | |
| <i>P. pusillus</i> | | | | | |
| dominant frequency | | | | | |
| Intercept | 7.17 | 7.13 | 7.21 | 378.6 | <0.001 |

| | | | | | |
|----------------|-------|-------|-------|------|--------------|
| (log) distance | -0.03 | -0.06 | -0.09 | -2.6 | 0.008 |
|----------------|-------|-------|-------|------|--------------|

3) Response:

P. bilineatus fischeri

dominant frequency

| | | | | | |
|-----------|------|------|------|--------|------------------|
| Intercept | 6.98 | 6.97 | 6.99 | 1445.2 | <0.001 |
|-----------|------|------|------|--------|------------------|

| | | | | | |
|----------------|-------|-------|--------|------|--------------|
| (log) distance | -0.01 | -0.01 | -0.002 | -2.5 | 0.012 |
|----------------|-------|-------|--------|------|--------------|

4) Response:

Ambient amplitude

1kHz

| | | | | | |
|-----------|-----|--------|--------|--------|------------------|
| Intercept | -70 | -73.43 | -67.26 | -44.69 | <0.001 |
|-----------|-----|--------|--------|--------|------------------|

| | | | | | |
|----------------|-------|-------|-------|-------|------------------|
| (log) distance | -3.95 | -5.36 | -2.55 | -5.53 | <0.001 |
|----------------|-------|-------|-------|-------|------------------|

5) Response:

P. subsulphureus

dominant frequency

| | | | | | |
|-----------|------|------|------|-------|------------------|
| Intercept | 7.25 | 7.23 | 7.28 | 632.2 | <0.001 |
|-----------|------|------|------|-------|------------------|

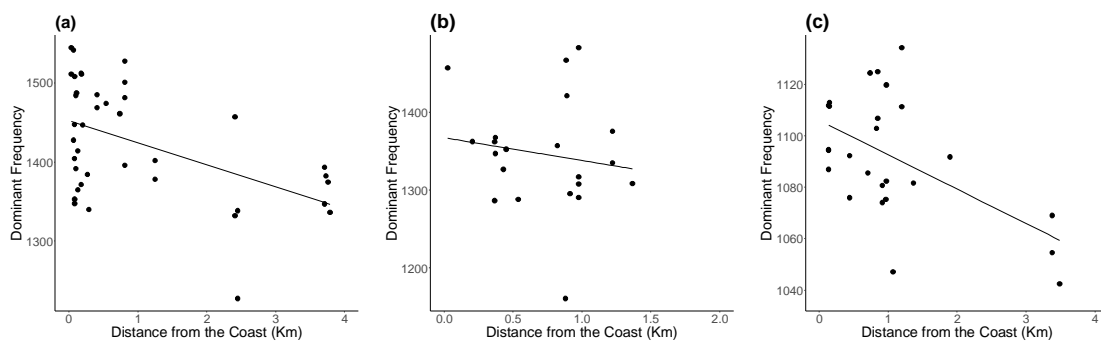
Ambient amplitude

1kHz

| | | | | |
|------|------|------|-----|------------------|
| 0.03 | 0.01 | 0.05 | 3.4 | <0.001 |
|------|------|------|-----|------------------|

245

246

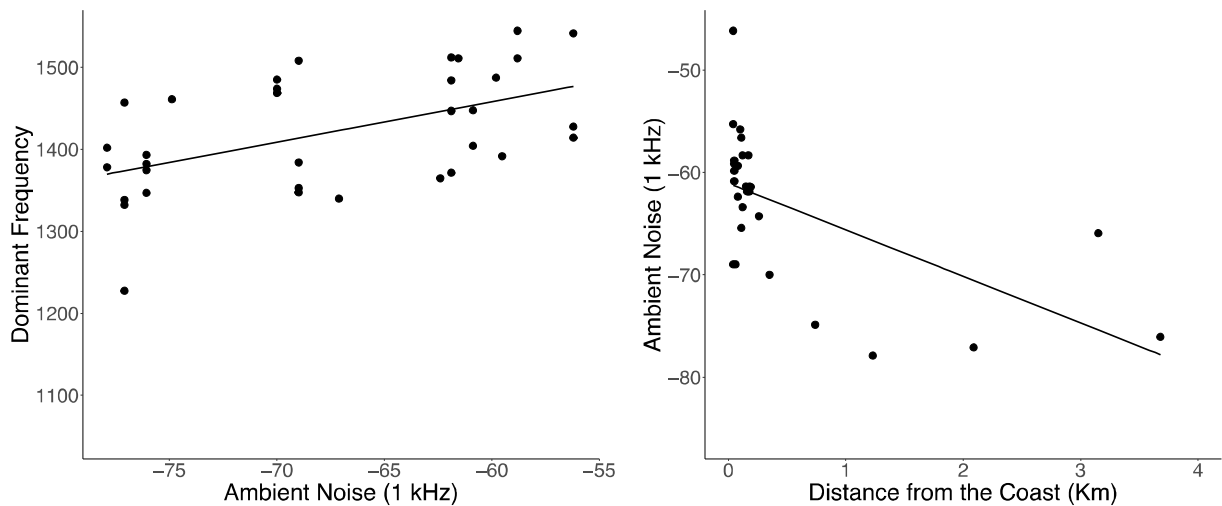


247

248 **Fig. 2** Plots showing the relationship between dominant frequency and distance from the
 249 coast in (a) *subsulphureus*, (b) *pusillus* and (c) *fischeri* before controlling for other possible
 250 effects.

251

252 Our results also show a strong significant decrease of low-frequency ambient noise
253 (1kHz) with log-distance from the coast in Cameroon as well as a significant positive
254 relationship between *subsulphureus* dominant frequency and ambient noise amplitude at
255 1kHz (Fig 3, Table 1).
256



257
258 **Fig. 3** Plots showing (a) the relationship between *subsulphureus* dominant frequency and
259 ambient noise and (b) between ambient noise and distance from the coast in Cameroon.

260

261 Discussion

262 We have shown that tinkerbirds sing at higher frequencies the closer they are to the coast and
263 as the amplitude of low-frequency ambient noise from ocean surf increases. Our results are in
264 line with the hypothesis that, as in the case of anthropogenic noise, natural ambient noise
265 affects acoustic signalling in birds (Kirschel et al. 2009a; Davidson et al. 2017). We show
266 that the masking effect of a natural low-frequency noise can affect vocalizations of animals
267 that lack the capacity to develop vocalisations through auditory feedback. Higher dominant
268 frequency may confer an adaptive advantage to coastal populations of the three species

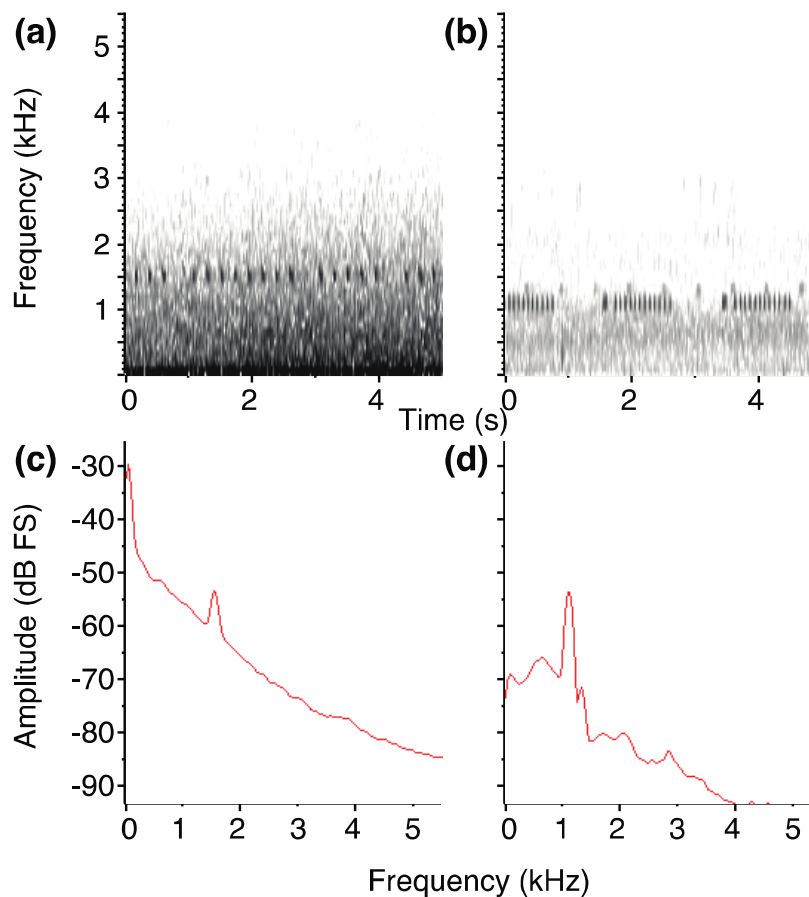
269 tinkerbirds because they benefit from increased transmission of signals to intended receivers.
270 Therefore, individuals with higher dominant frequency songs may have higher fitness at
271 coastal sites. Low frequency natural noise such as from ocean surf, rivers and waterfalls can
272 have a profound effect on auditory communication, as shown in concave-eared torrent frog
273 (*Amolops tormotus*), whose calls include ultrasound elements in their preferred habitat
274 alongside fast-flowing streams (Feng et al. 2006). Similar results have also been found in
275 another study, where support for the acoustic adaptation hypothesis has been demonstrated
276 when comparing torrent frogs to other species living in different habitats (Goutte et al. 2018).
277 Tinkerbirds are not restricted to such noisy environments, yet divergence in frequency
278 appears to occur in spite of ongoing gene flow with adjacent inland populations.

279 The pressure imposed by ocean surf low-frequency noise may have strong effects on
280 how species interact acoustically because of potential interference with their vocalizations in
281 the frequency domain. The effects of low-frequency ambient noise are likely to have a
282 stronger effect on species vocalizing at lower frequency and especially in birds that lack
283 vocal learning, such as tinkerbirds (Goodwin and Shriver 2011; Halfwerk et al. 2011). In this
284 study, *fischeri* is the species with the lowest dominant frequency and therefore may be
285 subjected to a greater pressure by ocean surf. In Kenya, it co-occurs with two other
286 *Pogoniulus* tinkerbirds: *P. pusillus* and eastern green tinkerbird *P. simplex* (hereafter
287 *simplex*), both of which sing at higher frequencies than *fischeri*. Indeed, *simplex* sings a
288 trilled song not unlike that of *fischeri*. It is therefore possible that continental populations of
289 *fischeri* are constrained to avoid the masking effect of low-frequency ocean surf sound by
290 increasing their dominant frequency because an increased pitch would result in greater
291 interference with the two competitors. Indeed, an increase in dominant frequency in
292 continental populations of *fischeri* could lead to song overlap in the frequency domain with
293 its two congeners (Fig. 4b). Stabilising selection might maintain *fischeri* song frequency at a

294 level that best reduces the masking effects of surf sound while maintaining sufficient
295 frequency differences between *fischeri* and other tinkerbird species. Coastal *fischeri* sing a
296 much faster trilled song than other forms of *P. bilineatus* (Nwankwo et al. 2018) and the
297 rapid repetition of pulses might itself be an adaptation to its sound environment in coastal
298 forests. An alternative hypothesis is that *fischeri* song might have evolved by convergent
299 character displacement to facilitate interspecific territoriality with *simplex* (e.g., Kirschel et
300 al. 2019). The observed increase of frequency in *fischeri* might also reflect the increase in
301 dominant frequency in *pusillus* song, as its frequency range may depend on *pusillus*
302 minimum frequency. Hence, the observed decreasing pattern in *fischeri* dominant frequency
303 with distance from the coast may in part be an effect of variation in *pusillus* song with
304 distance from the shore. A similar, if not stronger, correlation between frequency ranges is
305 expected to occur between *fischeri* and *simplex*, given the similarity of the song between the
306 two species. However, we did not have access to a suitable sample of *simplex* recordings to
307 test this hypothesis. Further work is needed to investigate the extent to which *fischeri* song
308 may also vary because of interactions with its congeners.

309 Higher dominant frequency have been suggested to be a consequence of an increased
310 song amplitude in non-passerines (Elemans et al. 2008; Nemeth and Brumm 2010; Nemeth et
311 al. 2012), whereas this is not always the case in passerines, which present higher vocal
312 flexibility (Zollinger et al. 2017). An increased amplitude can be an adaptation to noisy
313 environments according to the Lombard effect, which occurs when frequency range of the
314 vocalizing animal and the background noise overlap (Brumm and Todt 2002). In our study,
315 ocean surf sound widely overlaps with tinkerbirds song frequencies (Fig. 4), therefore one
316 possibility is that increased dominant frequency in tinkerbird song at coastal sites is a
317 consequence of raised vocal amplitude. The Lombard effect is a common trait in many bird
318 clades including passerines (Brumm and Todt 2002), Galliformes (Brumm et al. 2009) and

319 even in Paleognathae species such as tinamous (Schuster et al. 2012). The ancestral nature of
320 the Lombard effect suggests it occurs independently of the ontogeny of vocal learning in
321 birds (Brumm et al. 2009; Brumm and Zollinger 2011) and increased frequencies in
322 tinkerbird song might also be a consequence of increased vocal amplitude. This phenomenon
323 has been observed in other birds that lack song learning (Schuster et al. 2012). However, we
324 did not specifically test whether the increased dominant frequency occurs as a consequence
325 of the Lombard effect in tinkerbirds, but our results highlight this as a compelling area for
326 future investigations.
327



328
329 **Fig. 4** Figure showing the masking effect of ocean surf sound in spectrograms (a-b) and
330 power spectra profiles (c-d) of *subsulphureus* (left panels), *pusillus* and *fischeri* (right panels)
331 vocalizations, with *subsulphureus* song being recorded at 68 m from the shore and *pusillus*

332 and *fischeri* recording at 330 m.

333

334 Singing higher pitch songs in coastal sites may be an advantage in tinkerbirds, as higher
335 frequency songs often represent a selected trait by females (Hasegawa and Arai 2016). Also,
336 an increased pitch may result in an increased detectability by opposite-sex individuals.
337 Assuming that song frequency is correlated with amplitude, increased frequency would result
338 in a far-reaching signal which may further aid mate attraction. Similarly, in territorial
339 contests, higher pitch song may result in a larger active space (Brumm and Todt 2002) – a
340 potential advantage in territorial birds like tinkerbirds. However, pitch has been shown in
341 many birds to be negatively correlated with body size (Ryan and Brenowitz 1985; Brumm
342 and Goymann 2017, Kirschel et al. 2020, *in press*), whereas it does not seem to affect song
343 amplitude (Brumm 2009). Hence, any relative advantage in terms of signal transmission may
344 be counterbalanced by increased aggression from larger males, as higher frequency song may
345 be interpreted as a sign of weakness (Kirschel et al. 2020, *in press*). Ocean surf sound is a
346 continuous noise which pressure acts over evolutionary timescales on birdsong, therefore the
347 trade-offs between the potential advantages of increased mate attraction and at the same time
348 increased territorial response from other males may have had profound evolutionary
349 implications in shaping tinkerbird acoustic signals.

350 In this paper, we show that three tinkerbird species sing at a higher dominant frequency
351 the closer they are to the coastline. We suggest that low-frequency noise from ocean surf
352 imposes a selective pressure on tinkerbird acoustic signalling, and higher dominant frequency
353 songs may be selected because they reduce the masking effect of ocean surf sound. This
354 effect might be boosted if an increase in dominant frequency is accompanied by an increase
355 in amplitude. We predict that an increase in dominant frequency will occur but caution that
356 overlapping frequencies with related species might influence acoustic competition, as might

357 occur in *fischeri* where it coexists with *pusillus* and *simplex*. Our results show that natural
358 ambient noise has a similar impact to anthropogenic noise even on birds that do not learn
359 their songs, in line with the effects of natural ambient noise on oscine passerine vocalizations
360 (Davidson et al. 2017). We believe that our results can be extrapolated in other contexts of
361 background noise, including anthropogenic noise pollution, and therefore represent a baseline
362 for further studies on the effect of background noise on bird song.

363 **References**

- 364 Amador A, Goller F, Mindlin GB (2008) Frequency modulation during song in a suboscine
365 does not require vocal muscles. *J Neurophysiol* 99:2383–2389.
366 <https://doi.org/10.1152/jn.01002.2007>
- 367 Araya-Salas M (2020) baRulho: quantifying habitat-induced degradation of (animal) acoustic
368 signals in R
- 369 Beckers GJL, Suthers RA, Ten Cate C (2003) Mechanisms of frequency and amplitude
370 modulation in ring dove song. *J Exp Biol* 206:1833–1843.
371 <https://doi.org/10.1242/jeb.00364>
- 372 Bermúdez-Cuamatzin E, Ríos-Chelén AA, Gil D, Garcia CMÍ (2009) Strategies of song
373 adaptation to urban noise in the house finch: syllable pitch plasticity or differential
374 syllable use? *Behaviour* 146:1269–1286. <https://doi.org/10.1163/156853909X423104>
- 375 Blumstein DT, Mennill DJ, Clemins P, et al (2011) Acoustic monitoring in terrestrial
376 environments using microphone arrays: applications, technological considerations and
377 prospectus. *J Appl Ecol* 48:758–767. <https://doi.org/10.1111/j.1365-2664.2011.01993.x>
- 378 Bradbury JW, Vehrencamp SL (2011) *Principles of Animal Communication*, Second Ed. The
379 University of Chicago Press
- 380 Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB Balances Speed and
381 Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J*

- 382 9:378–400
- 383 Brumm H (2009) Song amplitude and body size in birds. *Behav Ecol Sociobiol* 63:1157–
384 1165. <https://doi.org/10.1007/s00265-009-0743-4>
- 385 Brumm H, Goymann W (2017) On the natural history of duetting in White-browed Coucals:
386 sex- and body-size-dependent differences in a collective vocal display. *J Ornithol*
387 158:669–678. <https://doi.org/10.1007/s10336-016-1429-0>
- 388 Brumm H, Naguib M (2009) Environmental Acoustics and the Evolution of Bird Song. In:
389 *Advances in the Study of Behavior*
- 390 Brumm H, Schmidt R, Schrader L (2009) Noise-dependent vocal plasticity in domestic fowl.
391 *Anim Behav* 78:741–746. <https://doi.org/10.1016/j.anbehav.2009.07.004>
- 392 Brumm H, Slabbekoorn H (2005) Acoustic Communication in Noise. *Adv Study Behav*
393 35:151–209. [https://doi.org/10.1016/S0065-3454\(05\)35004-2](https://doi.org/10.1016/S0065-3454(05)35004-2)
- 394 Brumm H, Slater PJB (2006) Ambient noise, motor fatigue, and serial redundancy in
395 chaffinch song. *Behav Ecol Sociobiol* 60:475–481. <https://doi.org/10.1007/s00265-006-0188-y>
- 396 0188-y
- 397 Brumm H, Todt D (2002) Noise-dependent song amplitude regulation in a territorial
398 songbird. *Anim Behav* 63:891–897. <https://doi.org/10.1006/anbe.2001.1968>
- 399 Brumm H, Zollinger A (2011) The evolution of the Lombard effect: 100 years of
400 psychoacoustic research. *Behaviour* 148:1173–1198.
401 <https://doi.org/10.1163/000579511X605759>
- 402 Brumm H, Zollinger SA, Niemelä PT, Sprau P (2017) Measurement artefacts lead to false
403 positives in the study of birdsong in noise. *Methods Ecol Evol* 8:1617–1625.
404 <https://doi.org/10.1111/2041-210X.12766>
- 405 Catchpole CK, Slater PJB (2008) *Bird song: biological themes and variation*, 2nd Editio.
406 Cambridge University Press, Cambridge, UK

- 407 Center for Conservation Bioacoustics (2019) Raven Pro: Interactive Sound Analysis
408 Software (Version 1.6) [Computer software]
- 409 Davidson BM, Antonova G, Dlott H, et al (2017) Natural and anthropogenic sounds reduce
410 song performance: insights from two emberizid species. *Behav Ecol* 28:974–982.
411 <https://doi.org/10.1093/beheco/axx036>
- 412 Deoniziak K, Osiejuk TS (2016) Disentangling Relations among Repertoire Size, Song Rate,
413 Signal Redundancy and Ambient Noise Level in European Songbird. *Ethology* 122:734–
414 744. <https://doi.org/10.1111/eth.12520>
- 415 Deoniziak K, Osiejuk TS (2019) Habitat-related differences in song structure and complexity
416 in a songbird with a large repertoire. *BMC Ecol* 19:1–11.
417 <https://doi.org/10.1186/s12898-019-0255-7>
- 418 Dominoni DM, Greif S, Nemeth E, Brumm H (2016) Airport noise predicts song timing of
419 European birds. *Ecol Evol* 6:6151–6159. <https://doi.org/10.1002/ece3.2357>
- 420 Dowsett-Lemaire F (1988) Fruit Choice and Seed Dissemination By Birds and Mammals in
421 the Evergreen Forests of upland Malawi. *Rev Ecol* 43:251–285
- 422 Elemans CPH, Zaccarelli R, Herzog H (2008) Biomechanics and control of vocalization in a
423 non-songbird. *J R Soc Interface* 5:691–703. <https://doi.org/10.1098/rsif.2007.1237>
- 424 Endler JA (1992) Signals, signal conditions, and the direction of evolution. *Am Nat*
425 139:S125–S153
- 426 Feng AS, Narins PM, Xu CH, et al (2006) Ultrasonic communication in frogs. *Nature*
427 440:333–336. <https://doi.org/10.1038/nature04416>
- 428 Francis CD, Ortega CP, Cruz A (2011) Different behavioural responses to anthropogenic
429 noise by two closely related passerine birds. *Biol Lett* 7:850–852.
430 <https://doi.org/10.1098/rsbl.2011.0359>
- 431 Gentry KE, McKenna MF, Luther DA (2018) Evidence of suboscine song plasticity in

- 432 response to traffic noise fluctuations and temporary road closures. *Bioacoustics* 27:165–
433 181. <https://doi.org/10.1080/09524622.2017.1303645>
- 434 Godschalk SKB (1985) Feeding behaviour of avian dispersers of mistletoe fruit in the Loskop
435 Dam Nature Reserve, South Africa. *South African J Zool* 20:136–146.
436 <https://doi.org/10.1080/02541858.1985.11447926>
- 437 Goodwin SE, Shriver WG (2011) Effects of traffic noise on occupancy patterns of forest
438 birds. *Conserv Biol* 25:406–411. <https://doi.org/10.1111/j.1523-1739.2010.01602.x>
- 439 Goutte S, Dubois A, Howard SD, et al (2018) How the environment shapes animal signals: a
440 test of the acoustic adaptation hypothesis in frogs. *J Evol Biol* 31:148–158.
441 <https://doi.org/10.1111/jeb.13210>
- 442 Halfwerk W, Bot S, Buix J, et al (2011) Low-frequency songs lose their potency in noisy
443 urban conditions. *Proc Natl Acad Sci U S A* 108:14549–14554.
444 <https://doi.org/10.1073/pnas.1109091108>
- 445 Halfwerk W, Lohr B, Slabbekoorn H (2018) Impact of man-made sound on birds and their
446 songs. In: *Effects of Anthropogenic Noise on Animals*. Springer, New York, NY
- 447 Halfwerk W, Ryan MJ, Wilson PS (2016) Wind- and rain-induced vibrations impose
448 different selection pressures on multimodal signaling. *Am Nat* 188:279–288.
449 <https://doi.org/10.1086/687519>
- 450 Halfwerk W, Slabbekoorn H (2009) A behavioural mechanism explaining noise-dependent
451 frequency use in urban birdsong. *Anim Behav* 78:1301–1307.
452 <https://doi.org/10.1016/j.anbehav.2009.09.015>
- 453 Harting F (2019) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
454 Regression Models
- 455 Hasegawa M, Arai E (2016) Female attraction to higher pitched male enticement calls in
456 Barn Swallows. *Ethology* 122:430–441. <https://doi.org/10.1111/eth.12492>

- 457 Hu Y, Cardoso GC (2010) Which birds adjust the frequency of vocalizations in urban noise?
458 *Anim Behav* 79:863–867. <https://doi.org/10.1016/j.anbehav.2009.12.036>
- 459 Kirschel ANG, Blumstein DT, Cohen RE, et al (2009a) Birdsong tuned to the environment:
460 Green hylia song varies with elevation, tree cover, and noise. *Behav Ecol* 20:1089–
461 1095. <https://doi.org/10.1093/beheco/arp101>
- 462 Kirschel ANG, Blumstein DT, Smith TB (2009b) Character displacement of song and
463 morphology in African tinkerbirds. *Proc Natl Acad Sci U S A* 106:8256–8261.
464 <https://doi.org/10.1073/pnas.0810124106>
- 465 Kirschel ANG, Nwankwo EC, Seal N, Grether GF (2020) Time spent together and time spent
466 apart affect song, feather colour and range overlap in tinkerbirds. *Biol J Linn Soc*
467 129:439–458. <https://doi.org/10.1093/biolinnean/blz191>
- 468 Kirschel ANG, Seddon N, Tobias JA (2019) Range-wide spatial mapping reveals convergent
469 character displacement of bird song. *Proc R Soc B Biol Sci* 286:17–19.
470 <https://doi.org/10.1098/rspb.2019.0443>
- 471 Kirschel ANG, Slabbekoorn H, Blumstein DT, et al (2011) Testing alternative hypotheses for
472 evolutionary diversification in an African songbird: rainforest refugia versus ecological
473 gradients. *Evolution* 65:3162–3174. [https://doi.org/https://doi.org/10.1111/j.1558-
474 5646.2011.01386.x](https://doi.org/https://doi.org/10.1111/j.1558-5646.2011.01386.x)
- 475 Kroodsma DE (1982) *Acoustic communication in birds*. Academic Press, New York
- 476 LaZerte SE, Otter KA, Slabbekoorn H (2017) Mountain chickadees adjust songs, calls and
477 chorus composition with increasing ambient and experimental anthropogenic noise.
478 *Urban Ecosyst* 20:989–1000. <https://doi.org/10.1007/s11252-017-0652-7>
- 479 Lazerte SE, Slabbekoorn H, Otter KA (2016) Learning to cope: vocal adjustment to urban
480 noise is correlated with prior experience in black-capped chickadees. *Proc R Soc B Biol*
481 *Sci* 283:. <https://doi.org/10.1098/rspb.2016.1058>

- 482 Lengagne T, Aubin T, Lauga J, Jouventin P (1999) How do king penguins (*Aptenodytes*
483 *patagonicus*) apply the mathematical theory of information to communicate in windy
484 conditions? Proc R Soc B Biol Sci 266:1623–1628.
485 <https://doi.org/10.1098/rspb.1999.0824>
- 486 Lengagne T, Slater PJB (2002) The effects of rain on acoustic communication: Tawny owls
487 have good reason for calling less in wet weather. Proc R Soc B Biol Sci 269:2121–2125.
488 <https://doi.org/10.1098/rspb.2002.2115>
- 489 Luther DA, Phillips J, Derryberry EP (2016) Not so sexy in the city: Urban birds adjust songs
490 to noise but compromise vocal performance. Behav Ecol 27:332–340.
491 <https://doi.org/10.1093/beheco/arv162>
- 492 Mendes S, Colino-Rabanal VJ, Peris SJ (2011) Bird song variations along an urban gradient:
493 The case of the European blackbird (*Turdus merula*). Landsc Urban Plan 99:51–57.
494 <https://doi.org/10.1016/j.landurbplan.2010.08.013>
- 495 Moseley DL, Derryberry GE, Phillips JN, et al (2018) Acoustic adaptation to city noise
496 through vocal learning by a songbird. Proc R Soc B Biol Sci 285:.
497 <https://doi.org/10.1098/rspb.2018.1356>
- 498 Naguib M, Riebel K (2014) Singing in space and time: the biology of birdsong. In:
499 Biocommunication of Animals. Springer
- 500 Naguib M, Wiley RH (2001) Review: Estimating the distance to a source of sound:
501 Mechanisms and adaptations for long-range communication. Anim Behav 62:825–837.
502 <https://doi.org/10.1006/anbe.2001.1860>
- 503 Nemeth E, Brumm H (2010) Birds and anthropogenic noise: Are urban songs adaptive? Am
504 Nat 176:465–475. <https://doi.org/10.1086/656275>
- 505 Nemeth E, Brumm H (2009) Blackbirds sing higher-pitched songs in cities: adaptation to
506 habitat acoustics or side-effect of urbanization? Anim Behav 78:637–641.

- 507 <https://doi.org/10.1016/j.anbehav.2009.06.016>
- 508 Nemeth E, Zollinger SA, Brumm H (2012) Effect sizes and the integrative understanding of
509 urban bird song: (A Reply to Slabbekoorn et al.). *Am Nat* 180:146–152.
510 <https://doi.org/10.1086/665994>
- 511 Nottebohm F (1972) The origins of vocal learning. *Am Nat* 106:116–140
- 512 Nwankwo EC, Pallari CT, Hadjioannou L, et al (2018) Rapid song divergence leads to
513 discordance between genetic distance and phenotypic characters important in
514 reproductive isolation. *Ecol Evol* 8:716–731. <https://doi.org/10.1002/ece3.3673>
- 515 Osmanski MS, Dooling RJ (2009) The effect of altered auditory feedback on control of vocal
516 production in budgerigars (*Melopsittacus undulatus*). *J Acoust Soc Am* 126:911–919.
517 <https://doi.org/10.1121/1.3158928>
- 518 Patricelli GL, Blickley JL (2006) Avian Communication in Urban Noise: Causes and
519 Consequences of Vocal Adjustment. *Auk* 123:639. [https://doi.org/10.1642/0004-8038\(2006\)123\[639:aciunc\]2.0.co;2](https://doi.org/10.1642/0004-8038(2006)123[639:aciunc]2.0.co;2)
- 520
- 521 Proppe DS, Avey MT, Hoeschele M, et al (2012) Black-capped chickadees *Poecile*
522 *atricapillus* sing at higher pitches with elevated anthropogenic noise, but not with
523 decreasing canopy cover. *J Avian Biol* 43:325–332. <https://doi.org/10.1111/j.1600-048X.2012.05640.x>
- 524
- 525 Proppe DS, Sturdy CB, St. Clair CC (2011) Flexibility in animal signals facilitates adaptation
526 to rapidly changing environments. *PLoS One* 6:1–4.
527 <https://doi.org/10.1371/journal.pone.0025413>
- 528 Ríos-Chelén AA, McDonald AN, Berger A, et al (2017) Do birds vocalize at higher pitch in
529 noise, or is it a matter of measurement? *Behav Ecol Sociobiol* 71:1–12.
530 <https://doi.org/10.1007/s00265-016-2243-7>
- 531 Ríos-Chelén AA, Salaberria C, Barbosa I, et al (2012) The learning advantage: bird species

532 that learn their song show a tighter adjustment of song to noisy environments than those
533 that do not learn. *J Evol Biol* 25:2171–2180. [https://doi.org/10.1111/j.1420-](https://doi.org/10.1111/j.1420-9101.2012.02597.x)
534 [9101.2012.02597.x](https://doi.org/10.1111/j.1420-9101.2012.02597.x)

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

537 Saranathan V, Hamilton D, Powell GVN, et al (2007) Genetic evidence supports song
538 learning in the three-wattled bellbird *Procnias tricarunculata* (Cotingidae). *Mol Ecol*
539 16:3689–3702. <https://doi.org/10.1111/j.1365-294X.2007.03415.x>

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

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

545 Seddon N (2005) Ecological adaptation and species recognition drives vocal evolution in
546 neotropical suboscine birds. *Evolution* 59:200–215

547 Short LL, Horne JFM (2002) Family Capitonidae (barbets). In: del Hoyo, J., Elliott, A.,
548 Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World*,
549 Vol. 7. Lynx Edicions, Barcelona, Spain, Barcelona, pp 140–219

550 Short LL, Horne JFM (2001) *Toucans, Barbets and Honeyguides*. Oxford University Press

551 Sierro J, Schloesing E, Pavón I, Gil D (2017) European blackbirds exposed to aircraft noise
552 advance their chorus, modify their song and spend more time singing. *Front Ecol Evol*
553 5:1–13. <https://doi.org/10.3389/fevo.2017.00068>

554 Slabbekoorn H (2013) Songs of the city: Noise-dependent spectral plasticity in the acoustic
555 phenotype of urban birds. *Anim Behav* 85:1089–1099.
556 <https://doi.org/10.1016/j.anbehav.2013.01.021>

- 557 Slabbekoorn H, den Boer-Visser A (2006) Cities Change the Songs of Birds. *Curr Biol*
558 16:2326–2331. <https://doi.org/10.1016/j.cub.2006.10.008>
- 559 Slabbekoorn H, Ripmeester EAP (2008) Birdsong and anthropogenic noise: implications and
560 applications for conservation. *Mol Ecol* 17:72–83. <https://doi.org/10.1111/j.1365-294X.2007.03487.x>
- 561
- 562 Slabbekoorn H, Smith TB (2002) Bird song, ecology and speciation. *Philos Trans R Soc B*
563 *Biol Sci* 357:493–503. <https://doi.org/10.1098/rstb.2001.1056>
- 564 Swaddle JP, Francis CD, Barber JR, et al (2015) A framework to assess evolutionary
565 responses to anthropogenic light and sound. *Trends Ecol Evol* 30:550–560.
566 <https://doi.org/10.1016/j.tree.2015.06.009>
- 567 Tolentino VC de M, Baesse CQ, Melo C de (2018) Dominant frequency of songs in tropical
568 bird species is higher in sites with high noise pollution. *Environ Pollut* 235:983–992.
569 <https://doi.org/10.1016/j.envpol.2018.01.045>
- 570 Touchton JM, Seddon N, Tobias JA (2014) Captive rearing experiments confirm song
571 development without learning in a tracheophone suboscine bird. *PLoS One* 9:.
572 <https://doi.org/10.1371/journal.pone.0095746>
- 573 Zollinger SA, Brumm H (2011) The Lombard effect. *Curr Biol* 21:R614–R615.
574 <https://doi.org/10.1016/j.cub.2011.06.003>
- 575 Zollinger SA, Podos J, Nemeth E, et al (2012) On the relationship between , and
576 measurement of , amplitude and frequency in birdsong. *Anim Behav* 1–9.
577 <https://doi.org/10.1016/j.anbehav.2012.04.026>
- 578 Zollinger SA, Slater PJB, Nemeth E, Brumm H (2017) Higher songs of city birds may not be
579 an individual response to noise. *Proc R Soc B Biol Sci* 284:.
580 <https://doi.org/10.1098/rspb.2017.0602>
- 581