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2 *[impairs the perception of song performance in blue tits and increases territorial response](#). *Animal**
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5

6 Keywords: Acoustic communication; Agression ; Auditory perception; Masking ; Noise pollution;
7 Playback; Urban conservation, song performance,

8 **Abstract**

9 Details in bird song parameters convey information about fitness, quality, and motivational state of
10 the signaller. Perception of these song details may affect decision making of receivers in territorial
11 defence and mate choice. Whether the message in the song is perceived or not may have major
12 consequences for the birds' reproductive success. Consequently, birds may suffer fitness
13 consequences from masking by other sounds in the environment. We conducted two different
14 playback experiments to test whether song consistency, a sexually selected performance
15 trait expressed in the temporal and spectral parameters of song, is perceived under different noise
16 conditions. In the first experiment, we found that blue tits (*Cyanistes caeruleus*) are less able to
17 assess the performance levels of song, but still detect the song stimuli under experimentally high
18 broad-band noise levels. Blue tits also responded more aggressively overall, independent of song
19 stimulus variation to playback of song stimuli under noisy conditions. In the second experiment, a
20 narrow-frequency band of noise at the same high amplitude levels **only affected response if it**
21 **spectrally overlapped with the song stimuli. Results from this experiment support the notion that it**
22 **is indeed the masking, rather than non-auditory effects of noise that cause the change in behaviour.**
23 Overall, our results show that there are noisy conditions which do not affect detection but still affect
24 perception of information in the detailed structure of songs. Not being able to discriminate or
25 respond appropriately to songs that differ in performance level is likely to have negative fitness
26 consequences and contribute to a detrimental impact of anthropogenic noise on individuals and
27 populations.

28 INTRODUCTION

29 Anthropogenic noise produced by transport and industry is widespread, pervasive, and detrimental
30 to wildlife (Francis & Barber, 2013; Jerem & Mathews, 2021; Shannon et al., 2016). One of the
31 negative impacts of anthropogenic noise is the masking effect it has on the acoustic communication
32 of animals (Brumm, 2004; Kleist, Guralnick, Cruz, & Francis, 2016; Wiley, 2006). While animals have
33 evolved to communicate in the presence of natural **ambient sound conditions** (Sebastianelli,
34 Blumstein, & Kirschel, 2021; Smith et al., 2013), anthropogenic noise differs from natural noise in
35 temporal, spectral and amplitude patterns (Barber, Crooks, & Fristrup, 2010). Adaptive responses
36 are therefore often problematic or impossible (Slabbekoorn, 2013; Wolfenden, Slabbekoorn, Kluk,
37 & de Kort, 2019).

38 Acoustic communication plays a critical role in many aspects of the life of birds, and any interference
39 in the **perception** of vocalisations can have fitness costs. These costs may include increased risk of
40 predation (Francis, Ortega, & Cruz, 2009; Lowry, Lill, & Wong, 2012), decreased breeding success as
41 a result of impaired parent-offspring communication (Halfwerk, Bot, Slabbekoorn, & Williams, 2012;
42 Leonard & Horn, 2008), suboptimal mate choice (Halfwerk, Holleman, Lessells, & Slabbekoorn,
43 2011) or failure to negate territorial conflicts leading to increased physical aggression (Wolfenden
44 et al., 2019). Consequently, many bird species appear to deploy strategies that counter the negative
45 effects of masking of their signals. Birds may change the timing of singing (Sierro, Schloesing, Pavon,
46 & Gil, 2017), the amplitude (Brumm, 2004), or the spectral structure of their songs (Slabbekoorn &
47 den Boer-Visser, 2006), all leading to masking release likely to improve the circumstances for
48 perception and an increase in the acoustic range of the signal (Brumm, 2004; Wiley, 2006).

49 Although many studies show how signallers are affected by, and respond to, increased noise levels,
50 much less is known about how receivers are affected, and how they might respond. What is known
51 so far through playback studies, is that territorial defence behaviours in response to conspecific song
52 are weaker (Kleist et al., 2016; Zwart, Dunn, McGowan, & Whittingham, 2016), or stronger in noisy
53 environments (Phillips & Derryberry, 2018; Wolfenden et al., 2019). Great tits (*Parus major*) exposed
54 to playback of conspecific alarm calls under traffic noise conditions responded less and slower
55 compared to quiet conditions (Templeton, Zollinger, & Brumm, 2016). Black-capped chickadees
56 (*Poecile atricapillus*) responded faster to playback of high-frequency songs than to low-frequency
57 songs under experimentally elevated traffic noise conditions that partially masked the latter

58 (LaZerte, Slabbekoorn, & Otter, 2017). What these studies have in common is that the receivers'
59 response is related to detection of the stimuli under different noise conditions. For instance, female
60 treefrogs (*Hyla ebraccata*) prefer male calls with a low carrier frequency, a preference they express
61 under quiet conditions. This preference changes to calls with high carrier frequency under noisy
62 conditions, presumably because the low frequency calls are masked by the noise and more difficult
63 to detect (Wollerman & Wiley, 2002).

64 However, for effective communication to take place, signals require more than detection. For
65 instance, one may be able to hear a human voice in a noisy environment (detect), and even be able
66 to tell the difference between two voices or utterances (discriminate), but that still does not mean
67 that one can understand what is being said (Carlile & Corkhill, 2015). Birds may be faced with similar
68 issues as birdsong can convey important information in subtle acoustic variation among variants of
69 the same signal type (Prior, Smith, Lawson, Ball, & Dooling, 2018), perhaps comparable to timbre
70 and intonation in human speech (Fishbein, Prior, Brown, Ball, & Dooling, 2021). These subtle
71 acoustic differences often convey information about the quality, fighting ability and motivation of
72 the singer and thus play an important role in mate choice and competition (Botero & de Kort, 2013;
73 Botero et al., 2009; de Kort, Eldermire, Cramer, & Vehrencamp, 2009; Podos, 1997; Slabbekoorn &
74 Ten Cate, 1998). The auditory thresholds for perceiving these details in the fine structure of acoustic
75 signals are higher than those for simple detection (Lohr, Wright, & Dooling, 2003).

76 Perceptual processes required for discriminating between signal variants are therefore likely
77 disrupted at lower noise levels compared to detection (Pohl, Leadbeater, Slabbekoorn, Klump, &
78 Langemann, 2012; Pohl, Slabbekoorn, Klump, & Langemann, 2009). Signal-to-noise levels often vary
79 with frequency and detection and processing of a particular signal will depend on the frequency
80 overlap with, and energy bias in noise spectra. Anthropogenic noise is typically characterised by
81 relatively high energy at low **frequencies** (Halfwerk et al., 2011), resulting in little overlap with oscine
82 song. Low-frequency noise may still mask higher frequencies through upward spread of masking
83 (Moore, 1997) and many studies have reported a noise related upward shift in oscine song
84 frequencies (Luther & Derryberry, 2012; Slabbekoorn & den Boer-Visser, 2006). For some species
85 and conditions, measuring methodology may have been an issue (Brumm, Zollinger, Niemelä, Sprau,
86 & Schielzeth, 2017), but importantly, whether this strategy improves detection, let alone
87 communication, through masking release has received only limited attention in natural settings
88 (Halfwerk et al., 2011; LaZerte et al., 2017). It has also been suggested that non-auditory effects of

89 noise may affect the response to stimuli through distraction rather than masking (Chou et al., 2023).
90 Hermit crabs (*Coenobita clypeatus*) responded slower to visual stimuli when exposed
91 simultaneously to noise, and this effect increased with level and duration of the noise (Chan et al.,
92 2010).

93 One song trait that functions as an indicator of vocal performance in birds is the ability to produce
94 virtually identical repetitions of songs or song components, referred to as song consistency (Botero
95 & de Kort, 2013; Sakata & Vehrencamp, 2012). Song consistency increases with age (Botero et al.,
96 2009; de Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009; Lambrechts & Dhondt, 1986;
97 Rivera-Gutierrez, Pinxten, & Eens, 2010), social status (Botero et al., 2009; Christie, Mennill, &
98 Ratcliffe, 2004), and better early-life conditions, in a number of species (Holveck, Vieira de Castro,
99 Lachlan, ten Cate, & Riebel, 2008; Lambrechts, 1997; Nowicki, Peters, & Podos, 1998). There is also
100 empirical evidence, in both banded wrens (*Thryophilus pleurostictus*) and great tits (*Parus major*),
101 that birds respond differentially to playback stimuli that vary only in song consistency (de Kort,
102 Eldermire, Valderrama, et al., 2009; Rivera-Gutierrez et al., 2010). In blue tits (*Cyanistes caeruleus*),
103 the songs of females are of lower vocal consistency than the songs of their social mates (Sierro, de
104 Kort, Riebel, & Hartley, 2022), and fertile females show a preference for male songs of high
105 consistency (Sierro, de Kort, & Hartley, 2023b). There is even evidence that song consistency plays
106 a role in extra-pair mating decisions as extra-pair mates in banded wrens sing more consistently
107 compared to the females' social mate (Cramer, Hall, de Kort, Lovette, & Vehrencamp, 2011).

108 In the current study, we aimed to test whether blue tits respond differentially to playback of songs
109 that differ in consistency-related performance level under different ambient noise conditions in two
110 sets of experiments. First, we tested for impact on detection and discrimination with broad
111 frequency bands of noise at different amplitude levels. Second, we tested for impact of noise on
112 detection and discrimination using two narrow bands of noise that differed in frequency range, one
113 that overlapped in frequency with the signal, and one that did not. The second experiment tested
114 whether blue tits' response to performance related stimuli is affected through distraction rather
115 than masking. We predicted that if there is only a masking effect of noise, the non-overlapping
116 narrow-frequency band of noise would not affect detection and discrimination but if noise distracts,
117 we expected a disruption of detection and/or discrimination in both.

118

119 METHODS

120 STUDY SITE AND POPULATION

121 Field trials were conducted during the breeding seasons in 2017 and 2018 using a nest-box
122 population of blue tits located on [REDACTED], United Kingdom (54°0' N, 02°7' W).
123 The site contains several woodland patches containing 120 wooden nest boxes that form part of
124 ongoing study into the breeding biology of blue tits (Leech, Hartley, Stewart, Griffith, & Burke, 2001;
125 Sierro et al., 2022). The majority of breeding blue tits in this population are colour ringed for
126 individual identification in the field.

127 Nest boxes were visited at least once every 4 days from the beginning of April to record first egg
128 date, assuming a laying rate of one egg per day (Cramp & Perrins, 1993; Mainwaring & Hartley,
129 2016). All playback trials were conducted on territorial males in whose nests egg laying had started.
130 This breeding phase corresponds to a period of high responsiveness towards conspecific song, as
131 blue tits are more motivated to guard their territory and mates from potential intruders, in order to
132 avoid extra pair copulations (Amrhein, Johannessen, Kristiansen, & Slagsvold, 2008), which in this
133 population occurs in approximately 40% of broods resulting in 11.7% of extra pair chicks (Leech et
134 al., 2001). **The study site is transected by the M6 motorway and therefore average noise exposure
135 at the nest boxes varies, and is relatively high, ranging from 49.7 dB(A) – 79.4 dB(A).** Trials were
136 performed on individuals whose nest boxes were located in relatively quiet areas, where the mean
137 noise levels did not exceed 55 dB(A) (Andrew Wolfenden, 2016, *unpublished data*). Ambient noise
138 measurements were taken in spring 2016 from the top of each nest box, using a Tenma 72-947 data-
139 logging sound-level meter (A-weighting, fast response, and 30–100 dB settings; accuracy ± 1.4 dB).

140 STIMULUS DESIGN

141 To test whether blue tits discriminate between levels of song performance under different noise
142 conditions, we created two sets of song stimuli that varied in level of consistency. As source for the
143 stimuli, we selected ten songs, each recorded from a different individual in the same study area in
144 2012 using a Marantz PMD661 and a Sennheiser ME67 microphone (WAVE format, 44.1 kHz
145 sampling rate, 16 bit amplitude encoding). Songs were selected from recordings with high signal-to-
146 noise ratio. A high-pass filter (> 1.0 kHz) was applied to remove low-frequency background noise
147 from the recordings using Avisoft-SASLab Pro (Specht, 2017).

148 Each unique song was manipulated in Avisoft-SASLab Pro to create a pair of song stimuli that
149 differed in level of consistency only, resulting in 10 unique stimulus pairs. Blue tit song consists of a
150 few high-frequency introductory notes, followed by a quick repetition of lower-frequency notes,
151 referred to as the trill (Fig. 1). All selected songs had three introductory notes followed by seven or
152 eight trill notes. Repetition of trill notes tend to become consistent from the third note in a trill
153 across a wide variety of bird species (Sierro, de Kort, & Hartley, 2023a). Therefore the 'consistent'
154 stimuli were generated by replacing all trill notes in the song with the 3rd trill note. This resulted in
155 a consistent song stimulus with a Spectral Cross Correlation value of 1 as measured with Avisoft-
156 CORRELATOR (Specht, 2017). For 'control' stimuli, original songs were used which were also
157 manipulated by cutting the trill notes from the original song and pasting them back in the same
158 order and rate (de Kort, Eldermire, Valderrama, et al., 2009). These trill-notes had a SPCC ranging
159 between 0.7 and 0.8. Fifteen copies of each manipulated song were used to create a song bout that
160 served as a playback stimulus, and songs within a playback bout were separated by an interval of
161 1.8 to 2.0 seconds, which is similar to the natural interval.

162 PLAYBACK PROCEDURE

163 The playback trials were carried out between 06:00h-12:00h and 18:00h-21:00h. In each trial
164 subjects were exposed to two playback treatments, namely consistent and control song stimuli with
165 order of treatment alternating between subjects. The output sound pressure level for both stimuli
166 was set at 64 dB(A), measured at 10 m from the loud speaker (FoxPro Fusion portable field speaker,
167 Lewistown, Pennsylvania 17044, USA) (Poesel, Pedersen, & Dabelsteen, 2004), using a sound
168 pressure level meter (Casella Cel-24X, fast response). Subsequent trials were never conducted on a
169 neighbouring territory within 48h. Trials were aborted whenever a subject was out of sight for
170 longer than 30s. The same subject was not re-tested within 24h. One trial consisted of 3 distinct
171 periods with a total duration of 480 s: a pre-playback period (60 s), followed by two playback periods
172 (210 s). Each playback period consists of 60 s of stimulus playback followed by 150 s of observation.
173 Response parameters were collected during the entire duration of the trial. Ten individuals were
174 tested twice under the two different experimental treatments (Experiment 1 and Experiment 2) in
175 different years.

176 During each trial, vocal behaviour and spoken observations of other behaviours by the subject were
177 recorded (WAVE format, 44.1 kHz sampling rate, 16 bit amplitude encoding) using a Marantz

178 PMD661 recorder and a Sennheiser ME67 (Wedemark, Lower Saxony, Germany). The following
179 response parameters were measured in each period: number of songs, time spent within a 5 m
180 radius from the speaker, number of flights directed towards the speaker, and response latency,
181 measured as the time (s) between the start of a stimulus and the first occurrence of a vocalisation
182 or flight. **Response behaviour of the subjects varies across the playback period. Following the start
183 of the playback stimulus, the subject often flies in the direction of the speaker and appears to be
184 actively looking for the source of the song stimulus by flying and hopping around the speaker. The
185 subject may also start singing or calling during this period. Most singing tends to happen after the
186 stimulus has finished. However, as with all behaviour, there is considerable variation between
187 individuals.**

188 EXPERIMENT 1 – NOISE LEVEL

189 In experiment 1, playback was conducted under **ambient** (No Noise), low-level noise (Noise) and
190 high-level noise (Loud Noise) conditions. Each subject was tested under only one noise condition.
191 All 3 conditions used the same 10 pairs of stimuli, but the Noise and Loud Noise conditions were
192 presented in combination with white noise (WAVE format, 44.1 kHz sampling rate, 16 bit amplitude
193 encoding), synthesised using the software Audacity (Audacity-Team, 2021). **Noise level increased
194 from the beginning of the pre-playback period to reach maximum level at 30 s before start of
195 playback 1 and continued for the entire duration of the trial.** The song stimuli were merged with the
196 white noise into a single sound file. The choice of full-spectrum white noise rather than a band-pass
197 filtered noise aimed at focusing exclusively on the effects of noise at different amplitude levels
198 excluding other potential factors.

199 The Noise condition had white noise superimposed at 25 dB root-mean-square (RMS) below the
200 maximum level of the stimulus (blue tit song), a value that in humans still allows for comfortable
201 speech recognition (Cooper & Cutts, 1971). The Loud noise condition had white noise superimposed
202 on the stimulus at 15 dB (RMS) below the maximum level of the stimulus. This signal-to-noise level
203 was based on the boundary of self-assessed comfortable listening to speech in human subjects in
204 the laboratory (Freyaldenhoven, Smiley, Muenchen, & Konrad, 2006; Rogers, Harkrider, Burchfield,
205 & Nabelek, 2003). **Both the Noise and Loud Noise conditions were above the signal detection
206 threshold for great tits** (Pohl et al., 2012). We assumed that field conditions in our study with blue

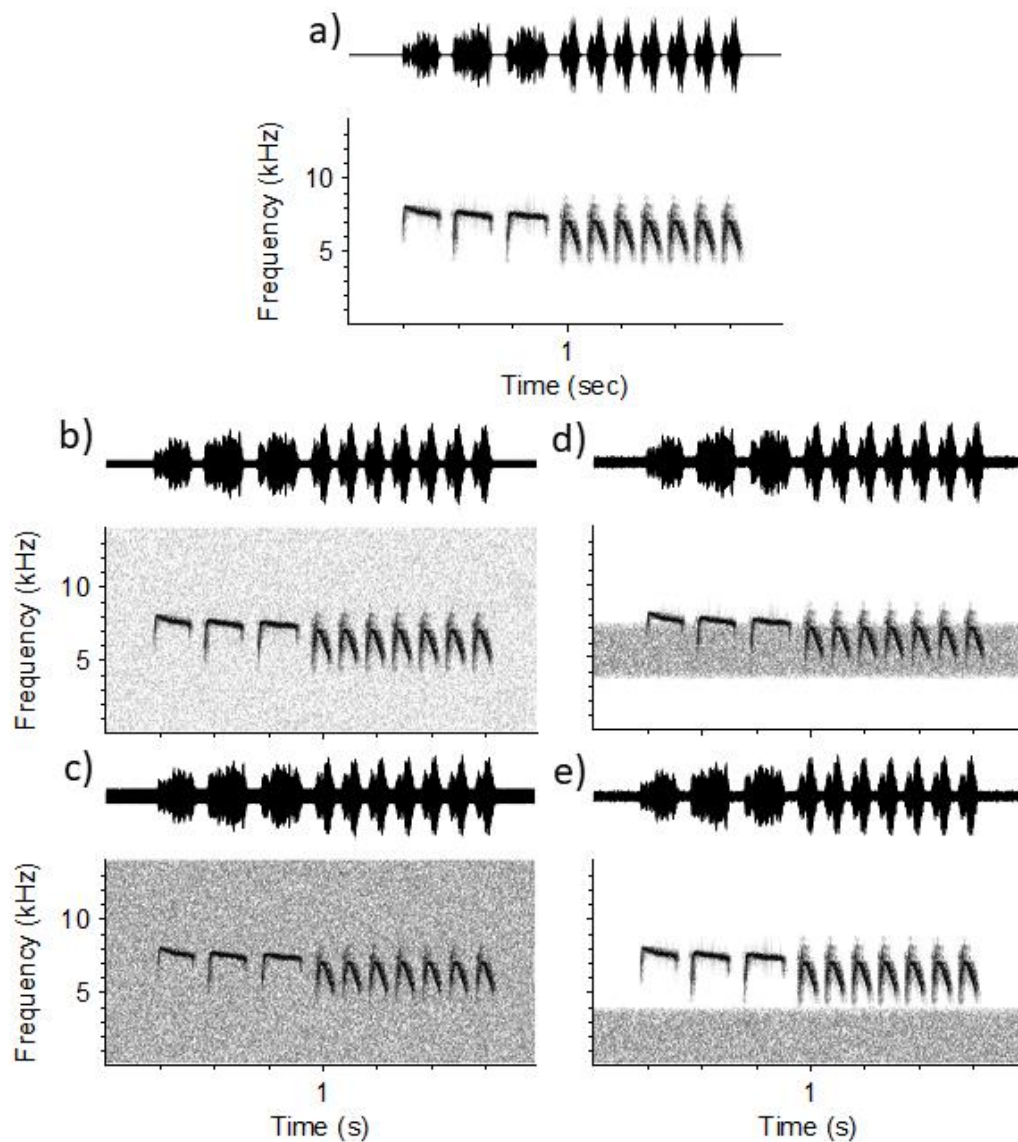
207 tits were less conducive to hearing the fine structure of acoustic signals in noise than those in
208 laboratory studies.

209 EXPERIMENT 2 – OVERLAPPING AND NON-OVERLAPPING NARROW BAND NOISE

210 In experiment 2, discrimination between playback stimuli was tested under spectrally overlapping
211 (Overlap) and non-overlapping (No overlap) noise conditions (Fig. 1). Masking noise levels for both
212 conditions were set at **the same amplitude as** in the Loud noise condition in experiment 1. **The No**
213 **Noise condition from Experiment 1 served as the control.** Each subject was tested for one noise
214 condition only.

215 In the Overlap trials, background noise overlapped the song stimuli in both the spectral and
216 temporal domains, while the No Overlap condition only overlapped in the temporal domain.
217 Frequency bandwidth of the song stimuli fell between 3530 - 7750 Hz. A masking noise with a
218 bandwidth of 3500 Hz was generated by band passing white noise with a roll-off of 6 dB per octave,
219 using the TDT PF1 module in Audacity software (Audacity-Team, 2021). This frequency distribution
220 was selected to allow for spectral overlapping of the trill, while also keeping the same bandwidth
221 for Overlap and No Overlap conditions. **Bird hearing is typically more sensitive in the frequencies of**
222 **their own songs (Henry & Lucas, 2008). In addition, the playback equipment is not capable of**
223 **producing frequencies close to 0Hz. Combined, these facts suggest that the lower frequency band**
224 **might be perceived as having a lower amplitude. On the other hand, birds, like humans, perceive**
225 **frequency not in a linear, but in a logarithmic scale (Cardoso, 2013), which implies that the lower**
226 **frequency band will be perceived as having a wider bandwidth. Theoretically, these issues would**
227 **lead to opposite but unspecified effects, and for that reason we decided to design our experiment**
228 **with frequency bands of the same absolute bandwidth.** For the Overlap condition, the bandpass
229 filter was set to 3670 - 7170 Hz, and for the No Overlap condition between 0 - 3500 Hz. Because
230 traffic noise is weighted towards lower frequencies (<1400 Hz) (Halfwerk et al., 2011), this
231 bandwidth resembles the frequencies encountered in noisy traffic conditions, **although the latter**
232 **have different spectral distribution of the power.**

233



234

235 Figure 1. Waveforms and spectrograms of blue tit song stimuli consisting of 3 introductory notes
 236 and 7 trill notes with noise superimposed a) Ambient sound condition that served as control for both
 237 experiment 1 with two noise conditions b) Noise c) Loud noise, and Experiment 2 with two noise
 238 conditions d) Spectrally overlapping high-frequency and e) Spectrally non-overlapping low-
 239 frequency. Spectrograms were created in Avisoft using the following parameters: Fast Fourier
 240 Transform 512, frequency resolution 8 Hz, Hamming window, overlap 8.

241 STATISTICAL ANALYSIS

242 For both experiments we fitted Linear Mixed-Effects Models (LMM) to test 1) whether the birds
 243 detected the playback in each noise condition and 2) whether the response to playback was
 244 different to consistent songs compared to control songs, depending on the noise treatment.

245 To test if birds detect the song stimuli under different noise conditions, we compared singing and
246 flying behaviour during the pre-playback and the 1st playback period. To that end we fitted two
247 models for experiment 1, one model with the number of songs per minute as a response variable,
248 and a second model with the number of flights per minute as a response variable. In the case of
249 singing behaviour, preliminary analysis showed that birds that were quiet before playback,
250 increased their singing activity following playback of conspecific song. However, many subjects were
251 detected by the experimenter through their singing behaviour and these birds had high vocal activity
252 during pre-playback and often reduced singing following the start of playback. Hence, we included
253 a binomial interaction term to define whether the bird was quiet (no songs) or was singing before
254 playback. We included the playback phase (pre- vs. post-playback) and the noise treatment as the
255 response variables. The noise treatment was a three-level categorical variable for experiment 1 (No
256 Noise, Noise, Loud Noise) and a two-level categorical variable for experiment 2 (Overlap, No
257 overlap).

258 To answer our second question, i.e. whether birds can discriminate between song treatments under
259 different noise conditions, we fitted four models with the number of songs per minute, the number
260 of flights per minute, the time spent within 5 m of the speaker and the latency to respond (flight or
261 song, whichever occurred first) as response variables in the two playback periods. The latency to
262 respond was log-transformed to approach normality. These models included the song treatment
263 and the noise treatment as explanatory variables. The song treatment was a two-level categorical
264 variable in both experiments (consistent vs. inconsistent control songs). The noise treatment was a
265 three-level categorical variable for both experiments: Experiment 1 (No Noise, Noise and Loud
266 Noise) and Experiment 2 (No Noise, Overlap and No overlap). In Experiment 2 we used the trials for
267 the No Noise condition from Experiment 1 as a control for the response of blue tits to consistent
268 and control stimuli under natural noise conditions. We also included a binomial categorical variable
269 with the order of song stimuli presentation to control for a possible bias. In all cases, the individual
270 identity was included as a random effect to avoid pseudo-replication and group observations within
271 trial. Given that the model was based on *a priori* experimental design, no model selection procedure
272 was applied.

273 All statistical analyses were carried out in R software 3.5.1 (Team, 2015). Packages used in the
274 statistical analysis were 'lme4'(Bates, Machler, Bolker, & Walker, 2015) and 'MuMIn' (Barton, 2011).

275 For data management and visualization we used 'stringr' (Wickham & Wickham, 2019), 'dplyr'
276 (Wickham, François, Henry, & Müller, 2022) and 'ggplot2' (Wickham, 2016).

277 Ethical note

278 'All fieldwork was approved by the [REDACTED] Ethics Committee and, where appropriate,
279 carried out under licences from Natural England (2016-22637, 2017-29455) and The British Trust
280 for Ornithology ([REDACTED]). Playback experiments were conducted on wild birds and an
281 individual was never tested more than 2 times in a single season with a total trial duration never
282 exceeding 10 minutes.

283

284 RESULTS

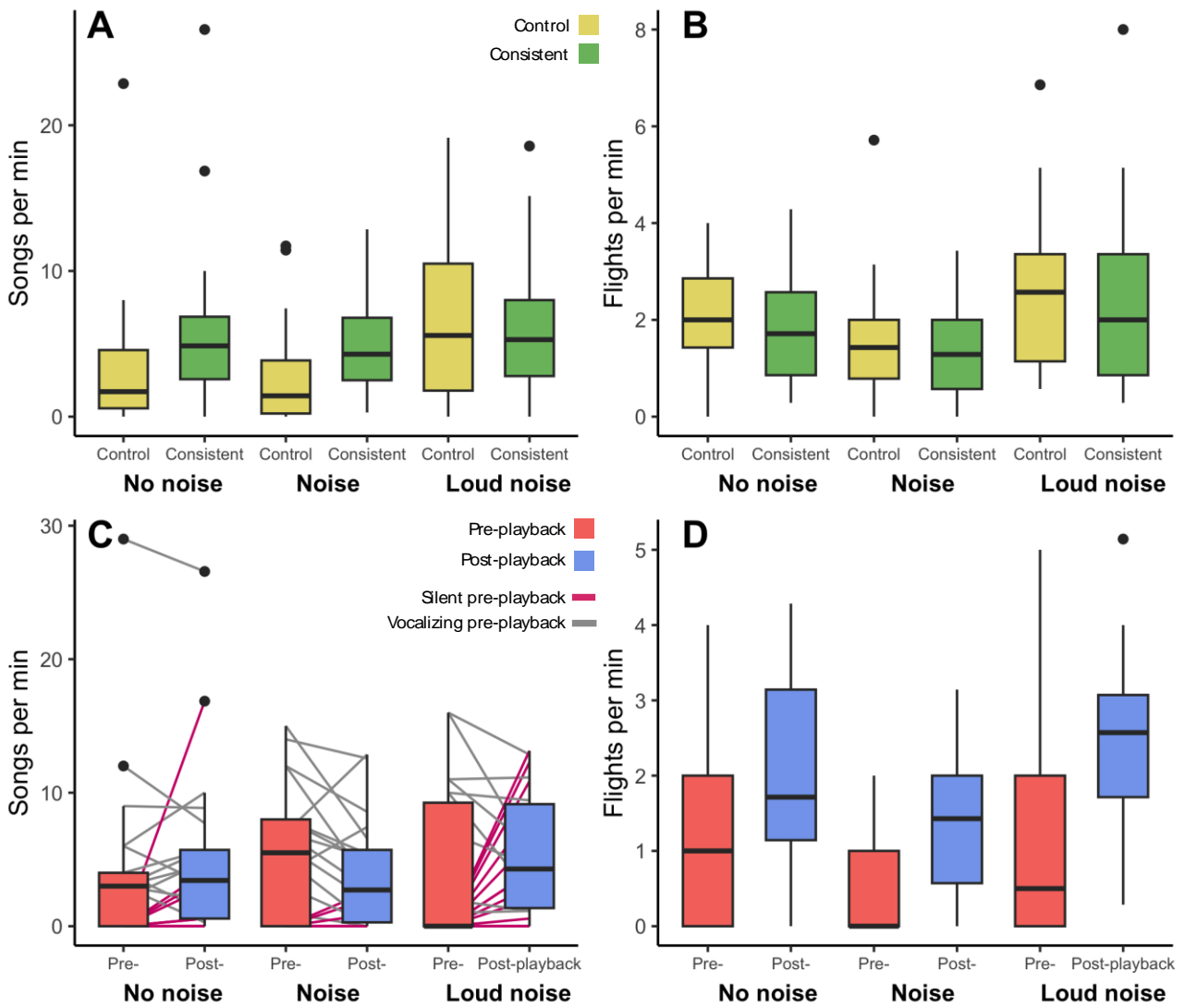
285 EXPERIMENT 1– NOISE LEVEL

286 In total, 65 individuals were tested for consistent and control stimuli in alternating order (21 in No
287 noise, 20 in Noise and 22 in Loud noise).

288 Detection of the stimuli was not affected by noise condition during playback: for all three noise level
289 conditions, blue tits significantly increased the number of flights and either increased or decreased
290 their song rate following the start of song playback (Table 2, Fig 2c & 2d). Discrimination between
291 the song stimuli was affected by noise level condition during playback. Blue tits produced more
292 songs following playback of consistent stimuli than following playback of control stimuli under the
293 No-Noise condition (Table 1, Fig. 2a). Such differential response towards the two song stimuli is
294 similar during the Noise condition. However, during the Loud noise condition, the response towards
295 control stimuli is significantly higher, which led to a significantly smaller difference in the response
296 towards control and consistent stimuli (Table 1, Fig 2a). In fact, when the Loud noise condition is set
297 as the reference level in the model, the results indicate there is no significant difference in song
298 response towards consistent and control stimuli in Loud noise conditions (Estimate: -0.77, 2.5% CI:
299 -6.96, 97.5% CI: 5.41, T: -0.24). No significant differences were observed in the other response
300 variables under any of the treatments (Table 1), although we found a non-significant trend that the
301 difference in latency to respond to consistent and inconsistent stimuli was reduced during the loud
302 noise condition, compared to the differences observed during the no noise condition.

303

304 For experiment 1, we did not find an effect of order of presentation in any of the response variables
305 (Table 1), although there was a non-significant trend for birds to respond faster (shorter response
306 latency) towards the second than towards the first presentation within a trial (Estimate: -0.36, 5%
307 CI: -0.68, 95% CI: -0.04).



308

309

310 Fig. 2 Difference in number of songs per minute (A) and number of flights per minute (B) in
311 response to conspecific song with control (yellow) or consistent stimuli (green) under different
312 noise treatments in blue tits (*Cyanistes caeruleus*). Blue tits sang significantly more in response to
313 consistent stimuli compared to control stimuli in No Noise, and Noise treatments but not in Loud
314 noise treatment. Blue tits detected the song stimuli in all noise conditions as shown by the change
315 in behaviour from pre-playback (red) to post-playback (blue) for number of songs (C) and number
316 of flights (D). Box and whisker plots show median, upper and lower quartiles, and 1.5 interquartile
317 range and outliers as points.

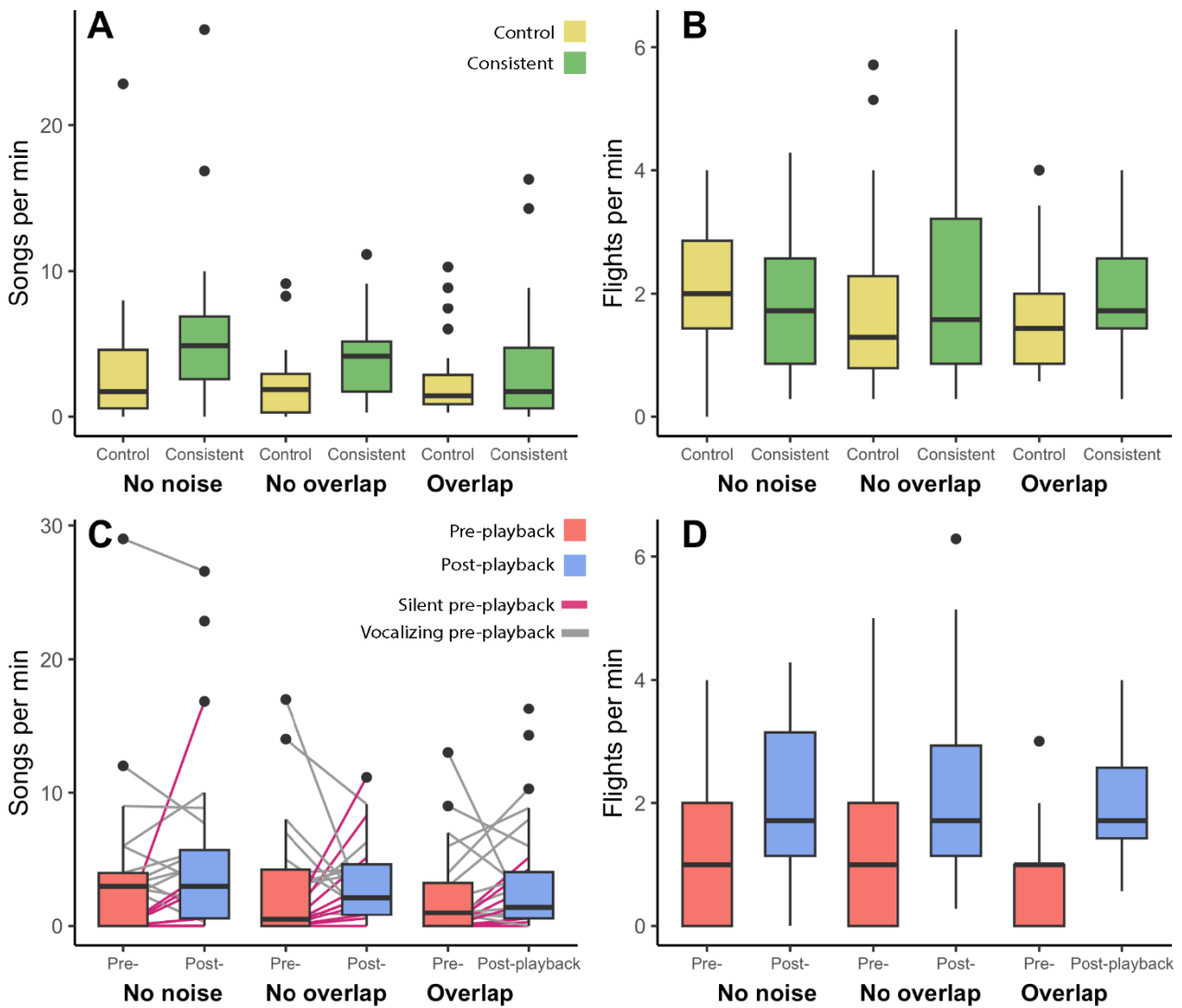
318 EXPERIMENT 2 – OVERLAPPING AND NON-OVERLAPPING NARROW-BAND NOISE

319 In total 40 individuals were tested in Experiment 2 (20 in each condition), which were compared to
320 the 21 trials under No Noise condition described in Experiment 1.

321 Detection of the stimuli was again not affected by noise condition during the first playback
322 presentation as blue tits showed a significant change in singing behaviour and an increase in the
323 number of flights following playback regardless of noise conditions (Table 4, Fig 3). The higher song
324 response towards consistent than towards control observed in No noise condition was similar during
325 the No overlap noise condition. However, we found a trend that such difference in response to
326 consistent and inconsistent stimuli was smaller during the Overlap noise condition (Table 3, Fig 3a).
327 In fact, when the Overlap noise condition is set as the reference level in the model, the results
328 indicate there is no significant difference in song response towards consistent and control stimuli in
329 Overlapping conditions (Estimate: 3.58, 2.5% CI: -1.12, 97.5% CI: 8.28, T: 1.47). No differences were
330 observed in the number of flights, or the time spent within 5 m of the speaker in relation to song
331 treatment (Fig 3., Table 3), but we found a non-significant trend that the latency to respond was
332 shorter towards consistent than inconsistent stimuli under the No Noise condition. In experiment
333 2, we found a significant effect of the order of presentation for number of flights and a non-
334 significant trend in the time spent within 5m, as the subjects tended to spend more time near the
335 speaker after the first compared to the second presentation (Table 3).

336

337



338

339 Fig. 3 Difference in number of songs (A) and number of flights (B) in response to conspecific song
 340 with control (yellow) and consistent (green) trill under different noise treatments in blue tits. **Note**
 341 **the No noise treatment shows the same data as experiment 1. The response was significantly higher**
 342 **towards consistent stimuli for the No Noise and No overlap noise condition, however such**
 343 **differential response disappears during the Overlap noise condition.** Blue tits detected all stimuli
 344 as shown by the significant change in singing (lines connect the same individual pre and post
 345 playback)(C) and flying (D) following conspecific stimuli under both noise condition. Box and whisker
 346 plots showing median, upper and lower quartiles, and 1.5 interquartile range and outliers as points.

347 **DISCUSSION**

348 During our playback experiments, blue tits always detected **the stimuli under any of the noise**
 349 **conditions by showing a change in behaviour following start of playback. However, they did not**
 350 **always discriminate (show a difference in response) between stimuli** that differed in performance
 351 level (consistency) when they were masked by relatively loud white noise. When the masking noise
 352 consisted of a narrow frequency band that did not spectrally **overlap with the blue tit song**, blue tits

353 detected and discriminated between song performance levels. **However, when the song stimuli**
354 **were presented in the presence of a spectrally overlapping noise band, blue tits did not discriminate**
355 **between stimuli of different performance level.** The lack of discrimination between song
356 performance levels in the loud white noise treatment may reflect realistic disruption of
357 communication under non-experimental anthropogenic noise levels in urban territories. Since song
358 plays an important role in mate choice and territorial conflict mediation, our results imply that such
359 noisy conditions may lead to suboptimal decision making in blue tits. Our results also showed that
360 under **broad frequency band noise** conditions, when blue tits were not able to assess simulated
361 competitors on their song performance, they were overall more aggressive.

362 **Masking-dependent discrimination**

363 The detection of a sound is the first step in the process of acoustic communication and requires a
364 relatively low signal-to-noise ratio (Lohr et al., 2003) **compared to discrimination.** For many signal
365 types, simple detection is sufficient to elicit the appropriate response from receivers, i.e. seeking
366 cover when hearing an alarm call (Templeton et al., 2016). Here we showed that when response
367 behaviour is based on discrimination between different renditions of the same signal type, such as
368 in mate choice or territorial disputes, noise may disrupt these processes. Since song plays an
369 important role in assessing competitors during territorial conflict, failing to show the appropriate
370 response to different competitors may result in injury, loss of territory tenancy (de Kort, Eldermire,
371 Cramer, et al., 2009) and paternity. Although these experiments were based on territorial
372 behaviour, it is likely that females making mate choice decisions will face similar difficulties with
373 discriminating between performance levels in song (Cramer et al., 2011; Sierro, de Kort, et al.,
374 2023b). Female blue tits roost inside the nesting cavity during the fertile period and can hear males
375 performing their dawn song, after which they emerge and chose a mating partner, which is often
376 not the social partner (Leech et al., 2001). Under quiet conditions, females show a preference for
377 songs with higher levels of consistency of trill notes (Sierro, de Kort, et al., 2023b), the kind of detail
378 in songs that we show here to be masked by noise.

379 Our results also show that in the presence of narrow band noise that spectrally overlaps the song at
380 the same level as the Loud Noise condition in experiment 1, the **masking effect of the noise although**
381 **still present, appears reduced.** One explanation for this might be that due to the spread of excitation
382 on the basilar membrane in the inner ear at higher sound levels in the song compared to the noise

383 (Moore, 1997), the song components important for consistency recognition could be detected in
384 the presence of narrow band noise using off-frequency listening (Patterson & Nimmosmith, 1980).
385 In other words, despite the spectral match between the song and narrow band noise, the song was
386 not completely masked by such noise, unlike the broadband white noise in experiment 1 that did
387 completely mask the potential for assessment of song performance. There appeared to be little
388 effect of upward masking (swamping) from noise spectra at frequencies lower than blue tit song as
389 the birds could discriminate between the stimuli when the narrow band noise did not overlap the
390 stimuli.

391 **Non-auditory effects of noise?**

392 In addition to the direct acoustic effect of noise, an alternative explanation for the lack of
393 discrimination between stimuli with different performance levels may be that noise distracts the
394 attention of the receiver (Chan et al., 2010). Noise energy spectrally matching the frequency of a
395 signal raises the auditory threshold for detection and discrimination more than noise that does not
396 match in frequency (Dooling & Blumenrath, 2013). However, the degree of distraction does not
397 depend on spectral overlap and may relate to overall noise level and predictability (Brumm &
398 Slabbekoorn, 2005; Naguib, 2013; Purser & Radford, 2011; Talling, Waran, Wathes, & Lines, 1998).
399 This is what we tested in our second experiment where we played narrow frequency band noise at
400 equivalent level to the Loud Noise condition in experiment 1, but spectrally overlapping, and non-
401 overlapping with the stimuli. Our results show that with spectrally overlapping narrow-band noise,
402 blue tits not only spend more time close to the loudspeaker compared to the non-overlapping noise
403 band treatment irrespective of the song performance level, but they were also unable to
404 discriminate between songs that differ in performance level. Discrimination between the stimuli
405 was not affected by the non-overlapping narrow band noise. Therefore, this study does not provide
406 support for the hypothesis that the distracting effect of noise causes a reduced capacity to
407 discriminate between the song stimuli, but instead that it should be attributed to the masking effect.

408 The stronger response to high- (consistent) compared to low-performance (control) song stimuli
409 was apparent in the number of songs the subjects sang in response to a simulated intruder. Birds
410 did not discriminate between high and low performance stimuli under loud conditions, instead they
411 sang indiscriminately with a higher song rate. They also showed a tendency to fly more in response
412 to stimuli under loud noise conditions. Under conditions when blue tits cannot hear the song stimuli

413 well, they increased their response strength irrespective of performance level of the playback
414 stimuli. This stronger response may be indicative of the phenomenon of ‘urban anger’ observed in
415 animals (Phillips & Derryberry, 2018; Slabbekoorn, 2013; Wolfenden et al., 2019) and humans
416 (Stansfeld & Matheson, 2003). The increased **response to intruders** in urban settings in birds has
417 been attributed to several factors, including increased lead exposure (McClelland et al., 2019),
418 selection that favours more **responsive** personality traits (Hardman & Dalesman, 2018) and
419 exposure to increased noise levels. However, these **distinct factors** are often difficult to disentangle
420 in an urban setting. Here we show that noise alone can increase **response intensity** (Chavez-
421 **Mendoza, Jose-Ramirez, & Rios-Chelen, 2023; Grabarczyk & Gill, 2019; Sierro, Sierro, & Slabbekoorn,**
422 **2023), which we interpret as being caused by an elevated level of agitation.** Non-auditory effects of
423 noise exposure, such as reduced capacity for communication, or over-stimulation can cause stress
424 and elevate agitation levels, perhaps resulting in more aggressive interactions, **although not all**
425 **studies showed similar results** (Reed et al., 2021; Zwart et al., 2016).

426 **Conclusions**

427 In many bird species, song plays a vital role in behaviours critical to and directly related to their
428 fitness, such as mate choice and territorial defence (Collins, 2004). The complexity and the structural
429 details of songs are what birds ultimately use to mediate sexual collaboration and conflict. Any
430 alteration in the perception of songs can therefore undermine optimal communication and lead to
431 suboptimal decision making with potentially significant fitness consequences. This study shows that
432 some of the fine structural details (trill consistency) can be masked by relatively high levels of white
433 noise, reflecting noisy conditions that frequently occur in territories of urban birds. The results of
434 this study add to a growing body of literature showing noise-induced changes in the behaviour of
435 receivers in natural conditions, in the context of mate-choice (Halfwerk et al., 2011; Halfwerk et al.,
436 2011; Huet des Aunay et al., 2014; Wollerman & Wiley, 2002), territorial defence (Kleist et al., 2016;
437 McMullen, Schmidt, & Kunc, 2014; Phillips & Derryberry, 2018), and parent-offspring
438 communication (Leonard, Horn, Oswald, & McIntyre, 2015; Lucass, Eens, & Muller, 2016). This study
439 highlights the importance of understanding the receiver’s role when studying the effects of noise
440 pollution on wildlife, not just in its ability to detect signals, but also in more complex processes such
441 as discrimination.

442

Table 1 – Differential response to playback song stimuli under different noise-level conditions, for experiment 1.

Response	Parameter	Estimate	2.5% CI	97.5% CI	T
No. of songs	Intercept ("Control", "No noise" and "1 st presentation")	11.184	3.611	18.757	2.847
	Song treatment: "Consistent" vs. "Control"	9.122	2.787	15.457	2.773
	Noise treatment: "Noise" vs "No noise"	-1.613	-12.117	8.892	-0.296
	Noise treatment: "Loud noise" vs "No noise"	10.583	0.326	20.84	1.992
	Order: "Second" vs. "First presentation"	0.557	-3.1	4.215	0.294
	Interaction - "Consistent" vs "Control" in "Noise"	-1.922	-10.99	7.146	-0.408
	Interaction - "Consistent" vs "Control" in "Loud noise"	-9.895	-18.749	-1.04	-2.152
No. of fights	Intercept	6.847	4.688	9.005	6.094
	Song treatment: "Consistent" vs. "Control"	-0.557	-2.961	1.846	-0.447
	Noise treatment: "Noise" vs "No noise"	-1.543	-4.457	1.371	-1.018
	Noise treatment: "Loud noise" vs "No noise"	1.78	-1.066	4.625	1.203
	Order: "Second" vs. "First presentation"	0.293	-1.095	1.681	0.406
	Interaction - "Consistent" vs "Control" in "Noise"	-0.243	-3.684	3.199	-0.136
	Interaction - "Consistent" vs "Control" in "Loud noise"	0.33	-3.03	3.69	0.189
Time within 5 m	Intercept	78.044	46.885	109.204	4.816
	Song treatment: "Consistent" vs. "Control"	1.944	-30.428	34.316	0.116
	Noise treatment: "Noise" vs "No noise"	-35.207	-77.627	7.214	-1.598
	Noise treatment: "Loud noise" vs "No noise"	11.634	-29.787	53.056	0.541
	Order: "Second" vs. "First presentation"	-15.175	-33.865	3.514	-1.564
	Interaction - "Consistent" vs "Control" in "Noise"	-4.194	-50.534	42.146	-0.174
	Interaction - "Consistent" vs "Control" in "Loud noise"	-8.535	-53.784	36.714	-0.363
Latency	Intercept	2.491	1.987	2.995	9.492
	Song treatment: "Consistent" vs. "Control"	-0.51	-1.165	0.146	-1.493
	Noise treatment: "Noise" vs "No noise"	-0.175	-0.838	0.488	-0.507
	Noise treatment: "Loud noise" vs "No noise"	-0.479	-1.126	0.169	-1.419
	Order: "Second" vs. "First presentation"	-0.358	-0.736	0.021	-1.815
	Interaction - "Consistent" vs "Control" in "Noise"	0.471	-0.467	1.409	0.964
	Interaction - "Consistent" vs "Control" in "Loud noise"	0.835	-0.081	1.751	1.750

Provided are model estimates, the associated 95% confident intervals (CI) and the *T* statistic. The reference levels for each categorical variable are shown in the first row for which the intercept is estimated. In this case the intercept shows the response control song stimuli for birds during no-noise condition in the first presentation within trial. For each categorical variable, the levels being compared are specified. If the parameter estimate is positive, it reflects a higher value for that level over the reference level. If the parameter estimate is negative, it reflects a higher value for that level respect to the reference level. The significance is derived from the 95% CI around the estimate, considering there is a significant effect if the 95% CI do not overlap with zero.

Table 2 – Stimuli detection under different noise -level conditions for experiment 1.

Response	Parameter	Estimate	2.5% CI	97.5% CI	Z
No. of songs	Intercept ("Pre-playback", "Silent", "No noise")	-0.287	-2.527	1.954	-0.246
	Phase: "Pre-" vs. "Post-playback"	3.5	1.985	5.015	4.525
	Vocalizing before: "Silent" vs. "Vocalising"	8.219	5.906	10.532	6.833
	Noise treatment: "Noise" vs. "No noise"	-0.628	-3.143	1.887	-0.481
	Noise treatment: "Loud noise" vs. "No noise"	0.907	-1.558	3.372	0.709
	Interaction - "Pre-" vs "Post-playback" in "Vocalizing pre-playback"	-5.488	-7.52	-3.456	-5.288
No. of fights	Intercept ("Pre-playback", "No noise")	0.995	0.564	1.427	4.473
	Phase: "Pre-" vs. "Post-playback"	1.029	0.689	1.37	5.968
	Noise treatment: "Noise" vs. "No noise"	-0.564	-1.134	0.007	-1.919
	Noise treatment: "Loud noise" vs. "No noise"	0.207	-0.35	0.764	0.723

Provided are model estimates, the associated 95% confident intervals (CI) and the T statistic. The reference levels for each categorical variable are shown in the first row for which the intercept is estimated. In this case the intercept shows the pre-playback behaviour during no-noise condition for birds that were silent before playback (reference levels at intercept for each categorical variable). For each categorical variable, the levels being compared are specified. If the parameter estimate is positive, it reflects a higher value for that level over the reference level. If the parameter estimate is negative, it reflects a lower value for that level respect to the reference level. The significance is derived from the 95% CI around the estimate, considering there is a significant effect if the 95% CI do not overlap with zero.

Table 3 – Differential response to playback song stimuli under different noise-level conditions for experiment 2.

Response	Parameter	Estimate	2.5% CI	97.5% CI	T
No. of songs	Intercept ("Control", "No noise" and "1 st presentation")	12.208	5.704	18.713	3.624
	Song treatment: "Consistent" vs. "Control"	9.029	4.559	13.498	3.888
	Noise treatment: "No overlap" vs "No noise"	-3.459	-12.571	5.652	-0.734
	Noise treatment: "Overlap" vs "No noise"	-1.76	-10.855	7.339	-0.374
	Order: "Second" vs. "First presentation"	-1.397	-4.03	1.236	-1.022
	Interaction - "Consistent" vs "Control" in "No overlap"	-3.229	-9.627	3.169	-0.971
	Interaction - "Consistent" vs "Control" in "Overlap"	-5.449	-11.923	1.03	-1.619
No. of fights	Intercept ("Control", "No noise" and "1 st presentation")	7.649	5.685	9.614	7.483
	Song treatment: "Consistent" vs. "Control"	-0.63	-2.643	1.382	-0.603
	Noise treatment: "No overlap" vs "No noise"	-0.73	-3.402	1.943	-0.525
	Noise treatment: "Overlap" vs "No noise"	-1.379	-4.04	1.28	-0.998
	Order: "Second" vs. "First presentation"	-1.24	-2.425	-0.054	-2.013
	Interaction - "Consistent" vs "Control" in "No overlap"	1.98	-0.901	4.862	1.323
	Interaction - "Consistent" vs "Control" in "Overlap"	1.63	-1.277	4.536	1.08
Time within 5 m	Intercept ("Control", "No noise" and "1 st presentation")	78.882	47.728	110.039	4.863
	Song treatment: "Consistent" vs. "Control"	1.868	-31.187	34.924	0.109
	Noise treatment: "No overlap" vs "No noise"	17.405	-24.817	59.627	0.793
	Noise treatment: "Overlap" vs "No noise"	-31.965	-73.929	10.071	-1.464
	Order: "Second" vs. "First presentation"	-16.775	-36.24	2.698	-1.659
	Interaction - "Consistent" vs "Control" in "No overlap"	-20.068	-67.387	27.251	-0.816
	Interaction - "Consistent" vs "Control" in "Overlap"	0.755	-46.865	48.541	0.03
Latency	Intercept ("Control", "No noise" and "1 st presentation")	2.408	1.944	2.871	9.967
	Song treatment: "Consistent" vs. "Control"	-0.502	-1.093	0.088	-1.637
	Noise treatment: "No overlap" vs "No noise"	-0.276	-0.887	0.335	-0.867
	Noise treatment: "Overlap" vs "No noise"	0.099	-0.505	0.703	0.314
	Order: "Second" vs. "First presentation"	-0.198	-0.546	0.149	-1.099
	Interaction - "Consistent" vs "Control" in "No overlap"	0.239	-0.606	1.085	0.545
	Interaction - "Consistent" vs "Control" in "Overlap"	-0.23	-1.075	0.62	-0.523

Provided are model estimates, the associated 95% confident intervals (CI) and the T statistic. The reference levels for each categorical variable are shown in the first row for which the intercept is estimated. In this case the intercept shows the response to control song stimuli for birds during overlap noise condition in the first presentation within trial. For each categorical variable, the levels being compared are specified. If the parameter estimate is positive, it reflects a higher value for that level over the reference level. If the parameter estimate is negative, it reflects a lower value for that level respect to the reference level. The significance is derived from the 95% CI around the estimate, considering there is a significant effect if the 95% CI do not overlap with zero.

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Table 4 – Stimuli detection under different noise-band conditions for experiment 2.

Response	Parameter	Estimate	2.5% CI	97.5% CI	Z
No. of songs	Intercept ("Pre-playback", "Silent", "No noise")	0.961	-1.166	3.088	0.869
	Phase: "Pre-" vs. "Post-playback"	<u>3.022</u>	<u>1.353</u>	<u>4.691</u>	<u>3.545</u>
	Vocalizing before: "Silent" vs. "Vocalising"	<u>5.741</u>	<u>3.523</u>	<u>7.959</u>	<u>4.974</u>
	Noise treatment: "No overlap" vs. "No noise"	-1.03	-3.358	1.297	-0.852
	Noise treatment: "Overlap" vs. "No noise"	-2.098	-4.426	0.231	-1.734
	Interaction - "Pre-" vs "Post-playback" in "Vocalizing pre-playback"	<u>-4.063</u>	<u>-6.266</u>	<u>-1.859</u>	<u>-3.61</u>
No. of fights	Intercept ("Pre-playback", "No noise")	1.008	0.537	1.479	4.149
	Phase: "Pre-" vs. "Post-playback"	<u>1.005</u>	<u>0.586</u>	<u>1.424</u>	<u>4.736</u>
	Noise treatment: "No overlap" vs. "No noise"	0.315	-0.293	0.922	1.006
	Noise treatment: "Overlap" vs. "No noise"	-0.139	-0.746	0.469	-0.444

Provided are model estimates, the associated 95% confident intervals (CI) and the T statistic. The reference levels for each categorical variable are shown in the first row for which the intercept is estimated. In this case the intercept shows the pre-playback behaviour during overlapping noise condition for birds that were silent before playback (reference levels at intercept for each categorical variable). For each categorical variable, the levels being compared are specified. If the parameter estimate is positive, it reflects a higher value for that level over the reference level. If the parameter estimate is negative, it reflects a lower value for that level respect to the reference level. The significance is derived from the 95% CI around the estimate, considering there is a significant effect if the 95% CI do not overlap with zero.

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453 REFERENCES

- 454 Amrhein, V., Johannessen, L. E., Kristiansen, L., & Slagsvold, T. (2008). Reproductive strategy and
455 singing activity: blue tit and great tit compared. *Behavioral Ecology and Sociobiology*, *62*(10),
456 1633-1641. doi: 10.1007/s00265-008-0592-6
- 457 Audacity-Team. (2021). Audacity(R): Free Audio Editor and Recorder (Version 3.0.0). Retrieved from
458 <https://audacityteam.org/>
- 459 Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial
460 organisms. *Trends in Ecology & Evolution*, *25*(3), 180-189. doi: 10.1016/j.tree.2009.08.002
- 461 Barton, K. (2011). MuMIn: Multi-model inference. R package (Version 1.0.0): Foundation for
462 Statistical Computing.
- 463 Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models
464 Using lme4. *Journal of Statistical Software*, *67*(1), 1-48. doi: DOI 10.18637/jss.v067.i01
- 465 Botero, C. A., & de Kort, S. R. (2013). Learned signals and consistency of delivery: a case against
466 receiver manipulation in animal communication. In U. Stegmann (Ed.), *Animal
467 Communication Theory: Information and Influence* (pp. 281-296). Cambridge: Cambridge
468 University Press.
- 469 Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., De Kort, S. R., & Vehrencamp,
470 S. L. (2009). Syllable Type Consistency is Related to Age, Social Status, and Reproductive
471 Success in the Tropical Mockingbird. *Anim Behav*, *77*(3), 701-706. doi:
472 10.1016/j.anbehav.2008.11.020
- 473 Brumm, H. (2004). The Impact of Environmental Noise on Song Amplitude in a Territorial Bird.
474 *Journal of Animal Ecology*, *73*(3), 434-440.
- 475 Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. In P. J. B. Slater, C. T.
476 Snowdon, H. J. Brockmann, T. J. Roper & M. Naguib (Eds.), *Advances in the Study of Behavior*,
477 *Vol 35* (Vol. 35, pp. 151-209). San Diego: Elsevier Academic Press Inc.
- 478 Brumm, H., Zollinger, S. A., Niemelä, P. T., Sprau, P., & Schielzeth, H. (2017). Measurement artefacts
479 lead to false positives in the study of birdsong in noise. *Methods in Ecology and Evolution*,
480 *8*(11), 1617-1625. doi: 10.1111/2041-210x.12766
- 481 Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel
482 inference in behavioral ecology: some background, observations, and comparisons.
483 *Behavioral Ecology and Sociobiology*, *65*(1), 23-35. doi: 10.1007/s00265-010-1029-6
- 484 Cardoso, G. C. (2013). Using frequency ratios to study vocal communication. *Animal Behaviour*,
485 *85*(6), 1529-1532. doi: 10.1016/j.anbehav.2013.03.044
- 486 Carlile, S., & Corkhill, C. (2015). Selective spatial attention modulates bottom-up informational
487 masking of speech. *Scientific Reports*, *5*. doi: ARTN 866210.1038/srep08662
- 488 Chan, A. A. Y.-H., David Stahlman, W., Garlick, D., Fast, C. D., Blumstein, D. T., & Blaisdell, A. P. (2010).
489 Increased amplitude and duration of acoustic stimuli enhance distraction. *Animal Behaviour*,
490 *80*(6), 1075-1079. doi: 10.1016/j.anbehav.2010.09.025
- 491 Chavez-Mendoza, N. E., Jose-Ramirez, S., & Rios-Chelen, A. A. (2023). Evidence that traffic noise
492 increases territorial response in vermilion flycatchers. *Frontiers in Ecology and Evolution*, *11*.
493 doi: ARTN 117573210.3389/fevo.2023.1175732
- 494 Chou, T. L., Krishna, A., Fossesca, M., Desai, A., Goldberg, J., Jones, S., . . . Gall, M. D. (2023).
495 Interspecific differences in the effects of masking and distraction on anti-predator behavior
496 in suburban anthropogenic noise. *Plos One*, *18*(8). doi: ARTN
497 e029033010.1371/journal.pone.0290330

- 498 Christie, P. J., Mennill, D. J., & Ratcliffe, L. M. (2004). Pitch shifts and song structure indicate male
 499 quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology*,
 500 55(4), 341-348. doi: 10.1007/s00265-003-0711-3
- 501 Collins, S. (2004). Vocal fighting and flirting: The functions of birdsong. In P. Marler & H. Slabbekoorn
 502 (Eds.), *Nature's music: the science of birdsong* (pp. 39-79). Amsterdam: Elsevier.
- 503 Cooper, J., J. C. , & Cutts, B. P. (1971). Speech discrimination in noise. *Journal of Speech and hearing*
 504 *Research*, 14, 332-337.
- 505 Cramer, E. R. A., Hall, M. L., de Kort, S. R., Lovette, I. J., & Vehrencamp, S. L. (2011). Infrequent Extra-
 506 Pair Paternity in the Banded Wren, a Synchronously Breeding Tropical Passerine. *The Condor*,
 507 113(3), 637-645. doi: 10.1525/cond.2011.100233
- 508 Cramp, S., & Perrins, C. M. (1993). *Handbook of the Birds of Europe, the Middle East, and North*
 509 *Africa: The Birds of the Western Palearctic Volume VII: Flycatchers to Shrikes*. Oxford: Oxford
 510 university Press.
- 511 de Kort, S. R., Eldermire, E. R. B., Cramer, E. R., & Vehrencamp, S. L. (2009). The deterrent effect of
 512 bird song in territory defense. *Behavioral Ecology*, 20(1), 200-206. doi:
 513 10.1093/beheco/arn135
- 514 de Kort, S. R., Eldermire, E. R. B., Valderrama, S., Botero, C. A., & Vehrencamp, S. L. (2009). Trill
 515 consistency is an age-related assessment signal in banded wrens. *Proceedings of the Royal*
 516 *Society B: Biological Sciences*, 276(1665), 2315-2321. doi: 10.1098/rspb.2009.0127
- 517 Dooling, R. J., & Blumenrath, S. H. (2013). Avian sound perception in noise. In H. Brumm (Ed.), *Animal*
 518 *Communication in Noise* (pp. 229-250). New York: Springer-Verlag.
- 519 Fishbein, A. R., Prior, N. H., Brown, J. A., Ball, G. F., & Dooling, R. J. (2021). Discrimination of natural
 520 acoustic variation in vocal signals. *Scientific Reports*, 11(1), 916. doi: 10.1038/s41598-020-
 521 79641-z
- 522 Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an
 523 urgent conservation priority. *Frontiers in Ecology and the Environment*, 11(6), 305-313.
- 524 Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise Pollution Changes Avian Communities and
 525 Species Interactions. *Current Biology*, 19(16), 1415-1419. doi: 10.1016/j.cub.2009.06.052
- 526 Freyaldenhoven, M. C., Smiley, D. F., Muenchen, R. A., & Konrad, T. N. (2006). Acceptable noise
 527 level: reliability measures and comparison to preference for background sounds. *Journal of*
 528 *the American Academy of Audiology*, 17(9), 640-648.
- 529 Grabarczyk, E. E., & Gill, S. A. (2019). Anthropogenic noise affects male house wren response to but
 530 not detection of territorial intruders. *Plos One*, 14(7). doi: ARTN
 531 e022057610.1371/journal.pone.0220576
- 532 Halfwerk, W., Bot, S., Buix, J., van der Velde, M., Komdeur, J., ten Cate, C., & Slabbekoorn, H. (2011).
 533 Low-frequency songs lose their potency in noisy urban conditions. *Proc Natl Acad Sci U S A*,
 534 108(35), 14549-14554. doi: 10.1073/pnas.1109091108
- 535 Halfwerk, W., Bot, S., Slabbekoorn, H., & Williams, T. (2012). Male great tit song perch selection in
 536 response to noise-dependent female feedback. *Functional Ecology*, 26(6), 1339-1347. doi:
 537 10.1111/j.1365-2435.2012.02018.x
- 538 Halfwerk, W., Holleman, L. J. M., Lessells, C. M., & Slabbekoorn, H. (2011). Negative impact of traffic
 539 noise on avian reproductive success. *Journal of Applied Ecology*, 48(1), 210-219. doi:
 540 10.1111/j.1365-2664.2010.01914.x
- 541 Hardman, S. I., & Dalesman, S. (2018). Repeatability and degree of territorial aggression differs
 542 among urban and rural great tits (*Parus major*). *Sci Rep*, 8(1), 5042. doi: 10.1038/s41598-
 543 018-23463-7

- 544 Henry, K. S., & Lucas, J. R. (2008). Coevolution of auditory sensitivity and temporal resolution with
545 acoustic signal space in three songbirds. *Animal Behaviour*, *76*, 1659-1671. doi:
546 10.1016/j.anbehav.2008.08.003
- 547 Holveck, M. J., Vieira de Castro, A. C., Lachlan, R. F., ten Cate, C., & Riebel, K. (2008). Accuracy of
548 song syntax learning and singing consistency signal early condition in zebra finches.
549 *Behavioral Ecology*, *19*(6), 1267-1281. doi: 10.1093/beheco/arn078
- 550 Huet des Aunay, G., Slabbekoorn, H., Nagle, L., Passas, F., Nicolas, P., & Draganoiu, T. I. (2014). Urban
551 noise undermines female sexual preferences for low-frequency songs in domestic canaries.
552 *Animal Behaviour*, *87*, 67-75. doi: 10.1016/j.anbehav.2013.10.010
- 553 Jerem, P., & Mathews, F. (2021). Trends and knowledge gaps in field research investigating effects
554 of anthropogenic noise. *Conservation Biology*, *35*(1), 115-129. doi: 10.1111/cobi.13510
- 555 Kleist, N. J., Guralnick, R. P., Cruz, A., & Francis, C. D. (2016). Anthropogenic noise weakens territorial
556 response to intruder s songs. *Ecosphere*, *7*(3), e01259. doi: 10.1002/ecs2.1259
- 557 Lambrechts, M. (1997). Song frequency plasticity and composition of phrase versions in great tits
558 *Parus major*. *Ardea*, *85*, 99-109.
- 559 Lambrechts, M., & Dhondt, A. A. (1986). Male quality, reproduction, and survival in the great tit
560 (*Parus major*). *Behavioral Ecology and Sociobiology*, *19*(1), 57-63.
- 561 LaZerte, S. E., Slabbekoorn, H., & Otter, K. A. (2017). Territorial black-capped chickadee males
562 respond faster to high- than to low-frequency songs in experimentally elevated noise
563 conditions. *Peerj*, *5*. doi: ARTN e325710.7717/peerj.3257
- 564 Leech, D. I., Hartley, I. R., Stewart, I. R. K., Griffith, S. C., & Burke, T. (2001). No effect of parental
565 quality or extrapair paternity on brood sex ratio in the blue tit (). *Behavioral Ecology*, *12*(6),
566 674-680.
- 567 Leonard, M. L., & Horn, A. G. (2008). Does ambient noise affect growth and begging call structure in
568 nestling birds? *Behav Ecol*, *19*. doi: 10.1093/beheco/arm161
- 569 Leonard, M. L., Horn, A. G., Oswald, K. N., & McIntyre, E. (2015). Effect of ambient noise on parent-
570 offspring interactions in tree swallows. *Animal Behaviour*, *109*, 1-7. doi:
571 10.1016/j.anbehav.2015.07.036
- 572 Lohr, B., Wright, T. F., & Dooling, R. J. (2003). Detection and discrimination of natural calls in masking
573 noise by birds: estimating the active space of a signal. *Animal Behaviour*, *65*(4), 763-777. doi:
574 10.1006/anbe.2003.2093
- 575 Lowry, H., Lill, A., & Wong, B. B. (2012). How noisy does a noisy miner have to be? Amplitude
576 adjustments of alarm calls in an avian urban 'adapter'. *PLoS One*, *7*(1), e29960. doi:
577 10.1371/journal.pone.0029960
- 578 Lucass, C., Eens, M., & Muller, W. (2016). When ambient noise impairs parent-offspring
579 communication. *Environ Pollut*, *212*, 592-597. doi: 10.1016/j.envpol.2016.03.015
- 580 Luther, D. A., & Derryberry, E. P. (2012). Birdsongs keep pace with city life: changes in song over
581 time in an urban songbird affects communication. *Animal Behaviour*, *83*(4), 1059-1066. doi:
582 10.1016/j.anbehav.2012.01.034
- 583 Mainwaring, M. C., & Hartley, I. R. (2016). Local weather conditions have complex effects on the
584 growth of blue tit nestlings. *J Therm Biol*, *60*, 12-19. doi: 10.1016/j.jtherbio.2016.05.005
- 585 McClelland, S. C., Duraes Ribeiro, R., Mielke, H. W., Finkelstein, M. E., Gonzales, C. R., Jones, J. A., . .
586 . Karubian, J. (2019). Sub-lethal exposure to lead is associated with heightened aggression in
587 an urban songbird. *Sci Total Environ*, *654*, 593-603. doi: 10.1016/j.scitotenv.2018.11.145
- 588 McMullen, H., Schmidt, R., & Kunc, H. P. (2014). Anthropogenic noise affects vocal interactions.
589 *Behav Processes*, *103*, 125-128. doi: 10.1016/j.beproc.2013.12.001
- 590 Moore, B. C. J. (1997). *An Introduction to the Psychology of Hearing*. San Diego: Academic Press.

- 591 Naguib, M. (2013). Living in a noisy world: indirect effects of noise on animal communication.
592 *Behaviour*, 150(9-10), 1069-1084. doi: 10.1163/1568539x-00003058
- 593 Nowicki, S., Peters, S., & Podos, J. (1998). Song learning, early nutrition and sexual selection in
594 songbirds. *American Zoologist*, 38, 179-190.
- 595 Patterson, R. D., & Nimmosmith, I. (1980). Off-Frequency Listening and Auditory-Filter Asymmetry.
596 *Journal of the Acoustical Society of America*, 67(1), 229-245. doi: Doi 10.1121/1.383732
- 597 Phillips, J. N., & Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait with
598 increased aggression in noise. *Sci Rep*, 8(1), 7505. doi: 10.1038/s41598-018-25834-6
- 599 Podos, J. (1997). A Performance Constraint on the Evolution of Trilled Vocalizations in a Songbird
600 Family (Passeriformes: Emberizidae) *Evolution*, 51(2), 537-551.
- 601 Poesel, A., Pedersen, S. B., & Dabelsteen, T. (2004). Dawn song of male blue tits as a predictor of
602 competitiveness in midmorning singing interactions. *Acta ethologica*, 6(2), 65-71. doi:
603 10.1007/s10211-004-0086-0
- 604 Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M., & Langemann, U. (2012). Great tits in
605 urban noise benefit from high frequencies in song detection and discrimination. [Article].
606 *Animal Behaviour*, 83(3), 711-721. doi: 10.1016/j.anbehav.2011.12.019
- 607 Pohl, N. U., Slabbekoorn, H., Klump, G. M., & Langemann, U. (2009). Effects of signal features and
608 environmental noise on signal detection in the great tit, *Parus major*. *Animal Behaviour*,
609 78(6), 1293-1300. doi: 10.1016/j.anbehav.2009.09.005
- 610 Prior, N. H., Smith, E., Lawson, S., Ball, G. F., & Dooling, R. J. (2018). Acoustic fine structure may
611 encode biologically relevant information for zebra finches. *Sci Rep*, 8(1), 6212. doi:
612 10.1038/s41598-018-24307-0
- 613 Purser, J., & Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces foraging
614 performance in three-spined sticklebacks (*Gasterosteus aculeatus*). *PLoS One*, 6(2), e17478.
615 doi: 10.1371/journal.pone.0017478
- 616 Reed, V. A., Toth, C. A., Wardle, R. N., Gomes, D. G. E., Barber, J. R., & Francis, C. D. (2021). Natural
617 noise affects conspecific signal detection and territorial defense behaviors in songbirds.
618 *Behavioral Ecology*, 32(5), 993-1003. doi: 10.1093/beheco/arab074
- 619 Rivera-Gutierrez, H. F., Pinxten, R., & Eens, M. (2010). Multiple signals for multiple messages: great
620 tit, *Parus major*, song signals age and survival. *Animal Behaviour*, 80(3), 451-459. doi:
621 10.1016/j.anbehav.2010.06.002
- 622 Rogers, D. S., Harkrider, A. W., Burchfield, S. B., & Nabelek, A. K. (2003). The influence of listener's
623 gender on the acceptance of background noise. *Journal of the American Academy of*
624 *Audiology*, 14(7), 372-382.
- 625 Sakata, J. T., & Vehrencamp, S. L. (2012). Integrating perspectives on vocal performance and
626 consistency. *J Exp Biol*, 215(Pt 2), 201-209. doi: 10.1242/jeb.056911
- 627 Sebastianelli, M., Blumstein, D. T., & Kirschel, A. N. G. (2021). Higher-pitched bird song towards the
628 coast supports a role for selection in ocean noise avoidance. *Bioacoustics*, 1-18. doi:
629 10.1080/09524622.2021.1879680
- 630 Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., . . . Wittemyer,
631 G. (2016). A synthesis of two decades of research documenting the effects of noise on
632 wildlife. *Biological Reviews*, 91(4), 982-1005. doi: 10.1111/brv.12207
- 633 Sierro, J., de Kort, S. R., & Hartley, I. R. (2023a). A limit to sustained performance constrains trill
634 length in birdsong. *Isience*, 26(11). doi: ARTN 10820610.1016/j.isci.2023.108206
- 635 Sierro, J., de Kort, S. R., & Hartley, I. R. (2023b). Sexual selection for both diversity and repetition in
636 birdsong. *Nat Commun*, 14(1), 3600. doi: 10.1038/s41467-023-39308-5

- 637 Sierro, J., de Kort, S. R., Riebel, K., & Hartley, I. R. (2022). Female blue tits sing frequently: a sex
638 comparison of occurrence, context, and structure of song. *Behavioral Ecology*, 33(5), 912-
639 925. doi: 10.1093/beheco/arac044
- 640 Sierro, J., Schloesing, E., Pavon, I., & Gil, D. (2017). European Blackbirds Exposed to Aircraft Noise
641 Advance Their Chorus, Modify Their Song and Spend More Time Singing. *Frontiers in Ecology
642 and Evolution*, 5. doi: 10.3389/fevo.2017.00068
- 643 Sierro, J., Sierro, J., & Slabbekoorn, H. (2023). Angry birds calling: an advanced system of signalling
644 aggression to moderate conflict in the common chiffchaff. *Animal Behaviour*, 201, 211-221.
645 doi: 10.1016/j.anbehav.2023.04.009
- 646 Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic
647 phenotype of urban birds. *Animal Behaviour*, 85(5), 1089-1099. doi:
648 10.1016/j.anbehav.2013.01.021
- 649 Slabbekoorn, H., & den Boer-Visser, A. (2006). Cities Change the Songs of Birds. *Current Biology*,
650 16(23), 2326-2331. doi: <https://doi.org/10.1016/j.cub.2006.10.008>
- 651 Slabbekoorn, H., & Ten Cate, C. (1998). Multiple parameters in the territorial coo of the collared
652 dove: Interactions and meaning. *Behaviour*, 135, 879-895. doi: Doi
653 10.1163/156853998792640323
- 654 Smith, T. B., Harrigan, R. J., Kirschel, A. N., Buermann, W., Saatchi, S., Blumstein, D. T., . . .
655 Slabbekoorn, H. (2013). Predicting bird song from space. *Evol Appl*, 6(6), 865-874. doi:
656 10.1111/eva.12072
- 657 Specht, R. (2017). Avisoft-SASLab Pro (Version 5.2). Berlin. Retrieved from
658 <https://www.avisoft.com/sound-analysis/>
- 659 Stansfeld, S. A., & Matheson, M. P. (2003). Noise-pollution: non-auditory effects on health. *British
660 Medical Bulletin*, 68, 243-257.
- 661 Talling, J. C., Waran, N. K., Wathes, C. M., & Lines, J. A. (1998). Sound avoidance by domestic pigs
662 depends upon characteristics of the signal. *Applied Animal Behaviour Science*, 58, 255–266.
- 663 Team, R. D. C. (2015). R: A language and environment for statistical computing. Vienna: R
664 Foundation for Statistical Computing.
- 665 Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm calls.
666 *Current Biology*, 26(22), R1173-R1174. doi: <https://doi.org/10.1016/j.cub.2016.09.058>
- 667 Wickham, H. (2016). ggplot2: Elegant graphics for data analysis R package.
- 668 Wickham, H., François, R., Henry, L., & Müller, K. (2022). A grammar of data manipulation (Version
669 1.0.10): R package.
- 670 Wickham, H., & Wickham, M. H. (2019). Package “stringr”. (Version 1.4.0): R package.
- 671 Wiley, R. H. (2006). Signal detection and animal communication. *Advances in the Study of Behavior*,
672 Vol 36, 36, 217-247. doi: 10.1016/S0065-3454(06)36005-6
- 673 Wolfenden, A. D., Slabbekoorn, H., Kluk, K., & de Kort, S. R. (2019). Aircraft sound exposure leads to
674 song frequency decline and elevated aggression in wild chiffchaffs. *J Anim Ecol*, 88(11), 1720-
675 1731. doi: 10.1111/1365-2656.13059
- 676 Wollerman, L., & Wiley, R. H. (2002). Background noise from a natural chorus alters female
677 discrimination of male calls in a Neotropical frog. (vol 63, pg 15, 2002). *Animal Behaviour*,
678 63, 1027-1027. doi: 10.1006/anbe.2002.3000
- 679 Zwart, M. C., Dunn, J. C., McGowan, P. J. K., & Whittingham, M. J. (2016). Wind farm noise
680 suppresses territorial defense behavior in a songbird. *Behavioral Ecology*, 27(1), 101-108.
681 doi: 10.1093/beheco/arv128